Universitat de les Illes Balears

TESI DOCTORAL

Del estudio de rasgos de vida a las estrategias de manejo: el caso del paíño europeo

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Memòria presentada per Ana Sanz Aguilar per optar al títol de Doctora del Programa de Doctorat de Biología Ambiental de la Universitat de les Illes Balears, sota la direcció dels Drs. Daniel Oro de Rivas, Giacomo Tavecchia i Eduardo Mínguez Díaz, i ponència del Dr. Rafael Bosch Zaragoza.

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A mi familia

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RESUMEN

Introducción

La teoría de la evolución de los rasgos de vida es un tema de interés fundamental en ecología, evolución y para la correcta identificación y ejecución de actuaciones de conservación o planes de manejo (Stearns 1992, Morris & Doak 2002). La respuesta de los parámetros demográficos al medio ambiente determina la dinámica de las poblaciones a nivel ecológico y la evolución de los rasgos de historias de vida a nivel evolutivo (Williams et al. 2002). Para comprender la dinámica de las poblaciones y lograr una conservación efectiva, se requiere establecer una conexión entre los procesos individuales y los procesos poblacionales (Tuljapurkar & Caswell 1997). Es imprescindible contar con estimas robustas que reflejen la variabilidad espacio-temporal de los parámetros demográficos y/o tasas de crecimiento poblacional (Coulson et al. 1999, Frederiksen et al. 2005); entender las bases evolutivas que regulan dichos parámetros (Sutherland 1996), así como estudiar las variaciones individuales (en función de edad, talla, fase de desarrollo, calidad intrínseca, etc) de los rasgos de vida (Stearns 1992). Ante un periodo de crisis de biodiversidad, causada en gran medida por factores de origen antrópico (Burney & Flannery 2005), la "biología de la conservación" (Soulé 1985) va a ser la ciencia encargada de afrontar la protección de la diversidad biológica en todos sus niveles (Soulé 1991). Para ello, es necesario disponer de herramientas científicas que permitan diagnosticar el estado conservación de especies o poblaciones y determinar y evaluar las acciones de conservación prioritarias (Morris & Doak 2002) en base al conocimiento que campos como la ecología del comportamiento y la teoría de la evolución de los rasgos de vida pueden aportar (Sutherland 1996, Lande 1988a). Las aves marinas son uno de los grupos donde su grado de amenaza se ha incrementado considerablemente durante las últimas décadas (Butchart et al. 2004). Se trata de especies longevas con bajas tasas reproductivas en las que la supervivencia adulta es el parámetro con mayor repercusión en la dinámica de sus poblaciones (Saether & Bakke 2000). En esta tesis doctoral se integran enfoques metodológicos, demográficos, ecológicos, evolutivos y de manejo aplicado a la conservación de un ave marina vulnerable, el paíño europeo (*Hydrobates pelagicus*). Se han recopilado datos de seguimiento individual a medio-largo plazo en seis colonias reproductoras localizadas en 5 islas mediterráneas que han permitido: a) evaluar las metodologías de monitoreo de poblaciones; b) obtener

estimas espacio-temporales de parámetros demográficos como la supervivencia, el reclutamiento y el éxito reproductor; c) realizar modelos poblacionales predictivos en base a las estimas obtenidas; d) estudiar los compromisos evolutivos entre reproducción y supervivencia y la influencia de variables individuales como la edad o la experiencia reproductora en los rasgos de vida; y e) planificar, llevar a cabo y evaluar la efectividad de las acciones de manejo encaminadas a aumentar la supervivencia adulta del paíño.

CAPÍTULO 1: Procesos de recaptura e inferencia biológica en el monitoreo de aves marinas con hábitos de cría hipogeos

El seguimiento de poblaciones de especies con hábitos de cría hipogeos es particularmente complicado. Generalmente sus densidades de población no pueden ser estimadas por censos de forma directa (Mitchell & Newton 2000). Para evaluar su estado de conservación y aproximarse al estudio de la dinámica de sus poblaciones se recurre habitualmente a la estimación de parámetros poblacionales mediante la modelización de datos de seguimiento individual a través de técnicas de captura-marcaje-recaptura, que asumen que existe una homogeneidad individual (Lebreton et al. 1992). En este capítulo se evaluaron los dos tipos de metodologías de captura comúnmente utilizadas en el seguimiento de aves (captura en redes vs. captura en nidos) para la estimación de parámetros poblaciones de interés (como el tamaño poblacional o la supervivencia). Se demostró que el nivel de heterogeneidad inter-individual y los consecuentes sesgos en la estima de parámetros dependía de la metodología empleada en la captura de las aves. El tipo de metodología de captura tuvo una fuerte influencia en la proporción de individuos transeúntes capturados, con importantes implicaciones en la fiabilidad de las estimas de tamaño poblacional (Kendall et al. 2004). Ninguno de los métodos analizados permitió obtener estimas robustas de tamaño poblacional. Se observó que la probabilidad de recaptura varió a lo largo del tiempo y entre las diferentes colonias y metodologías de captura, siendo especialmente alta en colonias donde las aves fueron capturadas en sus nidos mediante varias visitas anuales a las colonias. Tanto la captura de aves en redes como en nidos permitió obtener estimas fiables de supervivencia local. Las diferencias observadas en las probabilidades de supervivencia de las diferentes colonias parece

que respondieron a una variabilidad de origen natural, probablemente debida a diferentes presiones por depredación en las diferentes áreas de estudio, y no a la metodología de captura.

CAPÍTULO 2: Contrastando el reclutamiento y la supervivencia por edades a diferentes escalas espaciales: el paíño europeo como caso de estudio.

Los estudios evolutivos y las estrategias de conservación se derivan habitualmente de la generalización de patrones resultantes del análisis de una única población. Sin embargo, es habitual que los rasgos de vida presenten variaciones inter-poblacionales (Rodd & Reznick 1997, Frederiksen et al. 2005). En este capítulo se investigó la influencia de la edad en las probabilidades de reclutamiento, supervivencia y éxito reproductor del paíño; y cómo dichos parámetros variaban a diferentes escalas geográficas. Finalmente se analizó como las estimas de dichos parámetros afectarían a la tasa de crecimiento poblacional estimada mediante modelos de poblaciones estructurados por edades (Caswell 2001). Para ello se analizaron las historias de captura de 5523 paíños procedentes de tres colonias (dos en la isla de Benidorm y una en Marettimo). La supervivencia local, el reclutamiento y el éxito reproductor aumentaron con la edad en todas las colonias. A gran escala (Maretimo vs. Benidorm) se detectaron diferencias en supervivencia y reclutamiento. Sorprendentemente, también se encontraron diferencias a pequeña escala en los patrones de reclutamiento de las dos colonias adyacentes de la isla de Benidorm. Las diferencias inter-coloniales observadas en supervivencia y reclutamiento podrían reflejar la heterogeneidad espacial en la mortalidad debida a depredación, así como procesos específicos de cada colonia o dependientes de la densidad. De hecho, las diferencias en las tasas de supervivencia entre las dos islas desaparecieron al final del estudio respondiendo a la reducción de la depredación por parte de gaviotas especialistas en Benidorm. Los resultados del modelo poblacional sugirieron que diferentes combinaciones de parámetros demográficos pueden generar tasas de crecimiento poblacional esperado similares. El parámetro al que la tasa de crecimiento poblacional mostró una mayor sensibilidad fue la supervivencia adulta. Se concluyó que las acciones encaminadas a la conservación de esta especie deberían centrarse en aquellos factores que influencian la supervivencia adulta. Los resultados

presentados remarcaron la importancia de tener en cuenta la potencial heterogeneidad espacio-temporal de los rasgos de vida.

CAPÍTULO 3: El coste de la reproducción y los rasgos de vida dependientes de la experiencia en un pequeño petrel.

Desde un punto de vista evolutivo, la teoría de historias de vida predice que mayores inversiones de esfuerzo en la reproducción deberían acarrear mayores costes, que podrían expresarse en una reducción de la supervivencia o productividad; especialmente entre los individuos jóvenes e inexpertos que podrían no optimizar su inversión en la reproducción (Stearns 1992). En este capítulo se analizó, mediante modelos multiestado de captura-recaptura, cómo la experiencia reproductora y la inversión actual en la reproducción (entendida como el éxito reproductor de cada ave) se asociaban a la expresión de un coste de la reproducción en términos de una reducción de la supervivencia y/o del éxito reproductor futuros. Se encontró una relación positiva entre la inversión actual en la reproducción (el éxito reproductor actual), la experiencia reproductora y la supervivencia futura. El éxito reproductor se incrementó tras la adquisición de experiencia reproductora, pero fue independiente del éxito reproductor previo. No se detectó ningún coste asociado al esfuerzo reproductor. Los resultados sugirieron que el coste de la primera reproducción en relación a la supervivencia y la correlación positiva entre productividad y supervivencia podría deberse a una progresiva desaparición de los individuos de baja calidad (Barbraud & Weimerskirch 2006). Este trabajo hace hincapié en la necesidad de investigar simultáneamente el efecto de múltiples rasgos individuales en los estudios de compromisos evolutivos de historias de vida.

CAPÍTULO 4: Eliminación selectiva de un depredador facultativo basada en evidencias previas: eficacia y eficiencia

Las actividades humanas de las últimas décadas han modificado en gran medida las dinámicas depredador-presa en comunidades de aves marinas (Votier et al. 2004b). En concreto, las poblaciones de grandes gaviotas, depredadoras de especies de menor tamaño, han incremento sus densidades gracias a los aportes de alimento

procedentes de descartes pesqueros y vertederos (Oro et al. 1995). Para compensar este crecimiento, las agencias de conservación llevan a cabo programas de descaste masivo sin contar con información previa sobre su potencial afección sobre especies presa, por lo que generalmente resultan ineficientes e injustificados (Oro & Martínez-Abraín 2007). En base a los resultados obtenidos por Oro y colaboradores (2005) que alertaban de la afección de la depredación por parte de gaviotas patiamarillas (*Larus michahellis*) especialistas en la supervivencia del paíño, se realizó un programa de descaste selectivo de gaviotas especialistas. Se evaluaron los efectos del control de depredadores en la presión depredadora, probabilidades de supervivencia adulta y éxito reproductor del paíño europeo. Tras la eliminación selectiva de 16 gaviotas en tres años se produjo una reducción de alrededor de un 65% en el número de paíños depredado; y un incremento relativo de su supervivencia y éxito reproductor del 16% y 23%, respectivamente. Los resultados mostraron que unos pocos depredadores especialistas eran responsables de la mayor parte del impacto en una presa secundaria como el paíño, y su eliminación fue una medida de conservación efectiva para mejorar los parámetros demográficos de la especie presa.

Discusión general y perspectivas futuras.

Para lograr una conservación efectiva de especies en peligro es imprescindible partir de una diagnosis adecuada que integre información ecológica y evolutiva obtenida a través de métodos robustos y basar en ella las actuaciones de conservación. Los principales resultados obtenidos en esta tesis reflejan la existencia de variaciones espacio-temporales y de una influencia de la edad, la experiencia reproductora y la depredación por parte de gaviotas patiamarillas en los rasgos de vida del paíño europeo. Dado que altas tasas de mortalidad ponen en peligro la conservación de sus poblaciones, es necesario actuar sobre aquellas poblaciones que presenten niveles bajos de supervivencia adulta, siendo este parámetro estimable a partir de datos captura- recaptura obtenidos mediante la captura de nidos o gracias al uso de redes. La eliminación selectiva de gaviotas especialistas representa un método eficaz para mejorar el estado de conservación de la especie en poblaciones donde la mortalidad debida a depredación sea importante. En un futuro sería interesante evaluar el efecto de las condiciones ambientales, como los fenómenos climáticos o la

disponibilidad de alimento, en los parámetros demográficos de la especie; así como profundizar en el estudio de la heterogeneiodad inter-individual. La obtención de nuevos datos podría permitir la elaboración de modelos de poblaciones estructurados más complejos. En último termino, sería deseable coordinar los diferentes proyectos de monitoreo de la especie.

INTRODUCCIÓN

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LA EVOLUCIÓN DE LOS RASGOS DE VIDA:

DESDE LOS PROCESOS INDIVIDUALES A LA CONSERVACIÓN DE POBLACIONES.

En el corazón de la biología, la teoría de la evolución de los rasgos de vida representa un marco teórico clave para comprender la

> *"Nothing in biology makes sense except in the light of evolution (Dobzhansky 1973)"*

diversidad de formas de vida, la complejidad de sus ciclos de vida y la acción de los mecanismos evolutivos que actúan sobre ellas (Stearns 1992). Los organismos son lo que son, se comportan como se comportan, y viven donde viven debido a las especializaciones y restricciones impuestas por la historia evolutiva (Begon et al. 1996). La evolución de los rasgos de vida y de su plasticidad va a determinar la dinámica de poblaciones de las distintas especies que componen comunidades y ecosistemas (Stearns 1992, Williams et al. 2002).

El estudio de la dinámica de poblaciones es de interés fundamental en ecología, evolución y para la correcta identificación y ejecución de actuaciones de conservación o planes de manejo (Lande 1988a, Morris & Doak 2002, Sinclair et al. 2006). Las poblaciones son conjuntos de individuos de una determinada especie que coexisten en un tiempo y espacio determinado (Begon et al. 1996). Cuando una población se compone de varias subpoblaciones separadas en el espacio e interconectadas por fenómenos de dispersión y sujetas a

> *"Since population is a changing entity, we are interested not only in its size and composition at any one moment, but also how it is changing. (Odum 1971)"*

fenómenos de extinción y colonización, se denomina metapoblación (Hanski & Gilpin 1991). La dinámica poblacional analiza las causas de los cambios en la densidad y estructura de las poblaciones en el espacio y en el tiempo (Krebs 2001). Estos cambios son el resultado acumulativo del comportamiento o acciones de los individuos que las componen (de Roos 1997, Sutherland 1996).

Los individuos nacen, crecen, se desarrollan, maduran, se mueven, se reproducen y mueren. Estos procesos individuales describen el desarrollo de los individuos a lo largo de su ciclo de vida y están sujetos a la selección natural (Begon et al. 1996, Kokko & López-Sepulcre 2007). Rara vez, todos los individuos presentes en una

población son iguales. Generalmente existen variaciones individuales en sus rasgos de vida dependiendo de su edad, talla, fase de desarrollo, calidad intrínseca o genotipo, jerarquía social, etc. (Stearns 1992, Begon et al. 1996, Sutherland 1996). Además, en aquellas poblaciones localizadas en ambientes espaciales heterogéneos pueden existir importantes variaciones espaciales en los rasgos de vida (Coulson et al. 1999).

Mediante el seguimiento individualizado de un número representativo de individuos en una población a lo largo del tiempo se pueden obtener estimas de sus parámetros demográficos (reproducción, supervivencia, dispersión) en función de sus características individuales (edad, estatus, talla, etc.) y del tamaño poblacional (Williams et al. 2002). Sin embargo, es relativamente habitual que los seguimientos individuales presenten "historias incompletas", es decir, que la probabilidad de observación de los individuos sea imperfecta. En estos casos, la probabilidad de detección de los individuos puede incorporarse en modelos de captura-marcaje-recaptura (Seber 1982, Lebreton et al. 1992, Nichols 1992, Williams et al. 2002). Los modelos más simples, "uniestado", permiten estimar las probabilidades de recaptura, supervivencia, reclutamiento y tamaño poblacional en base a historias individuales donde únicamente se incluye la información de si un individuo ha sido capturado u observado o no en una determinada ocasión (Seber 1982, Lebreton et al. 1992, Lebreton et al. 1995, Pradel & Lebreton 1999, Nichols et al. 2000, Tavecchia et al. 2001). Mediante modelos más complejos, como los "multiestado", se puede estimar el movimiento entre diferentes estados que pueden incorporar información biológica adicional (reclutamiento o paso de un estado "pre-reproductor" a uno "reproductor", frecuencia reproductora o movimiento entre un estado "reproductor" a uno "no-reproductor", etc.) o espacial (dispersión) (Lebreton et al. 1999, Kendall & Nichols 2002, Lebreton & Pradel 2002, Tavecchia et al. 2002, Lebreton et al. 2003, Cam et al. 2004, Schaub et al. 2004, Barbraud et al. 2006). Tan importante como conocer los parámetros demográficos de las poblaciones y su variación en el tiempo y en el espacio, es entender las bases evolutivas que regulan dichos parámetros (Sutherland 1996). Los modelos multiestado de captura-recaptura son especialmente relevantes en estudios evolutivos ya que permiten analizar simultaneamente los compromisos entre rasgos de vida en poblaciones naturales (Cam & Monnat 2000, Barbraud et al. 2006, Gimenez et al. 2008). El último avance en modelización de datos de captura-

recaptura lo representan los modelos "multievento", que permiten incorporar incertidumbre en la asignación de los estados (Pradel 2005). Los modelos de captura-recaptura son una herramienta clave para la estimación de parámetros demográficos y tamaño poblacional, siempre y cuando se respeten las asunciones implícitas de cada modelo específico y los datos sean de calidad (Pradel 1993, Hardgrove & Borland 1994, Pradel et al. 1997, Kendall 1999, Link 2004).

Las tasas con las que los procesos demográficos (natalidad, mortalidad, inmigración y emigración) se producen son las que van a determinar el futuro de la población: si crece, decrece, se expande, se contrae, fluctúa, se mantiene estable y, finalmente, si persistirá o se extinguirá en un tiempo dado (Tuljapurkar & Caswell 1997, Williams et al. 2002). Los factores ambientales tanto de tipo biótico (interacciones intra- e interespecíficas) como abiótico (características físico-químicas del medio, procesos climáticos, catástrofes, etc.) afectarán a las poblaciones a través de sus efectos en los procesos individuales o parámetros demográficos de sus componentes (Begon et al. 1996). Las poblaciones tienen el potencial de crecer exponencialmente, pero los recursos son generalmente limitados por lo que la selección natural penalizará a aquellos individuos que peor compitan o que peores estrategias adopten para maximizar su eficacia biológica (*fitness*) en cada situación determinada (Stearns 1992, Sutherland 1996). En el mundo real las poblaciones animales rara vez muestran patrones de crecimiento simples tales como los descritos para los modelos clásicos como el exponencial o logístico (Lebreton & Clobert 1991, Sibly & Hone 2002). Para modelizar la dinámica de una población, y su respuesta al medio ambiente, se requiere establecer una conexión entre los procesos individuales o demográficos y las dinámicas poblacionales. Esta conexión puede establecerse gracias a los modelos poblacionales (Tuljapurkar & Caswell 1997, Beissinger & McCullough 2002).

La respuesta de los parámetros demográficos al medio ambiente determina la dinámica de las poblaciones a nivel ecológico y la evolución de los rasgos de historias de vida a nivel evolutivo (Caswell 2001, Williams et al. 2002). Sin embargo, este no es un proceso unidireccional ya que las poblaciones también

> *"Evolution itself only makes sense when viewed in its ecological context (Coulson et al. 2006, Saccheri & Hanski 2006, Johnson & Stinchcombe 2007, Metcalf & Pavard 2007, Pelletier et al. 2007)".*

influyen en el medio (Kokko & López-Sepulcre 2007). Conforme cambian las poblaciones (por ejemplo sus densidades) sus efectos en el medio varían (por ejemplo la cantidad de recursos disponibles) y consecuentemente se modifican las presiones de selección que actúan sobre los procesos demográficos (reproducción, supervivencia) generando, de nuevo, cambios poblacionales. La persistencia en el tiempo y el espacio de poblaciones, especies y comunidades, es decir su conservación, va a depender de procesos tanto ecológicos como evolutivos (Lande 1988a).

LA CRISIS ACTUAL DE LA BIODIVERSIDAD

La extinción de especies o pérdida de diversidad biológica, es un proceso natural, tal y como lo es la aparición de nuevas especies (Gould 1980). Durante la historia de la vida en la tierra han existido periodos de crisis de biodiversidad, también denominados "extinciones en masa", en los que se han producido numerosas extinciones en periodos de tiempo relativamente cortos, es decir, en unos pocos millones de años (Stanley 1986). Los procesos de extinción en masa ocurridos con anterioridad a la aparición del hombre en la Tierra, han sido atribuidos a agentes catastróficos como el impacto de meteoritos; vulcanismo; glaciaciones; variaciones en la salinidad, nivel de oxígeno o nivel del mar; y cambios climáticos (Raup 1986). Sin embargo, tras el crecimiento de las poblaciones humanas y su expansión desde África y Europa hacia otros continentes, el hombre se ha convertido en una de las principales causas de extinción actuales (Burney & Flannery 2005). La tasa de extinción actual, estimada entre 1000 y 10000 veces superior a la tasa natural esperada (Pimm et al. 1995, IUCN 2007), pone de manifiesto que nos encontramos ante un periodo de crisis de biodiversidad, definido como una *"sexta extinción en masa"* (Leakey & Levin 1995, Thomas et al. 2004), causada o amplificada por factores de origen antrópico (Meffe & Carroll 1997, Burney & Flannery 2005). La transformación de hábitats, sobreexplotación de especies, contaminación, introducción de especies exóticas y el cambio climático han sido consideradas las principales causas de la pérdida actual de Biodiversidad (Ehrlich 1988, Diamond 1989, Soulé 1991, Primack 1995, Vitousek et al. 1997, Western 2001, Jenkins et al. 2003, Millenium Ecosystem Assessment 2005, Malcolm et al. 2006, Root & Schneider 2006).

LA BIOLOGÍA DE LA CONSERVACIÓN

Como respuesta de la comunidad científica ante este preocupante escenario surge la "biología de la conservación"; una nueva ciencia de carácter multidisciplinar destinada a frenar la pérdida de biodiversidad y establecer relaciones sostenibles entre las comunidades humanas y el medio ambiente (Soulé 1985, Primack 1995, Meffe & Carroll 1997). Su meta principal es proteger la diversidad biológica en todos sus niveles; desde los genes a los ecosistemas pasando por poblaciones, especies y comunidades sin dejar de lado el mantenimiento de tradiciones y prácticas culturales humanas integradas históricamente en los ecosistemas (Soulé 1991). Para ello es necesario mantener la composición, estructura y funcionamiento de los sistemas biológicos (integridad ecológica) y asegurar su capacidad de persistir en el tiempo (salud ecológica) (Callicott et al. 1999).

La biología de la conservación nació como una disciplina de crisis encaminada a la toma de decisiones en base a la información científica y recursos disponibles en el menor tiempo posible, pero se ha consolidado como una aproximación multidisciplinar dirigida al estudio y al manejo de las poblaciones amenazadas (Soulé 1986, Pullin 2002). Ante esta reciente aproximación multidisciplinar surge la necesidad de integrar todo el bagaje teórico existente en los diferentes campos de estudio que la componen, así como desarrollar herramientas analíticas adecuadas. Todavía hoy, la biología de la conservación carece de un marco teórico sólido. El conocimiento que campos como la ecología del comportamiento y la teoría de la evolución de los rasgos de vida pueden aportar a la conservación está, todavía, poco explotado (Sutherland 1996, Martínez-Abraín & Oro, in prep). A este respecto, la teoría de la evolución de los rasgos de vida puede proporcionar un marco teórico que ayude a la toma de decisiones, ya que para predecir el futuro de las poblaciones son indispensables tanto los conocimientos ecológicos como evolutivos (Lande 1988a).

Siendo los recursos en conservación limitados, los gestores de la naturaleza se encuentran ante un problema importante: la necesidad de optimizar los recursos en actuaciones de conservación que garanticen resultados (Myers et al. 2000). Habitualmente los esfuerzos de conservación se concentran a nivel de especies y/o

poblaciones, en particular, sobre aquellas que se encuentran amenazadas o median procesos ecológicos importantes (Soulé 1991, Soulé 1987). Sin embargo, no es raro que para muchas especies o poblaciones, se desconozca el riesgo real de desaparición o declive, los puntos débiles de su biología, o las causas de su limitada distribución, abundancia o regresión de sus poblaciones. Ante este escenario, se hace necesario disponer de herramientas científicas que permitan diagnosticar el estado conservación de especies o poblaciones; identificar cuáles son los parámetros demográficos deprimidos y sus causas de declive en poblaciones en regresión; y determinar las acciones de conservación prioritarias y más eficaces (Krebs 2001, Morris & Doak 2002, Norris 2004). Para asignar a las especies a categorías que reflejen su riesgo relativo de extinción existen criterios cuantitativos basados en el tamaño de sus poblaciones, los rasgos de vida de la especie, sus tasas de declive y su área de distribución (IUCN 2001). Sin embargo, pocas veces una especie entra a formar parte de una determinada categoría de amenaza tras haberse realizado valoraciones de su viabilidad basadas en datos empíricos obtenidos tras largas series de monitorización del área de ocupación o del ciclo biológico completo (Schemske et al. 1994). Además, en muchos casos los resultados son inciertos; ya sea por la dificultad de identificar las actuaciones de conservación prioritarias y su grado de eficacia tras su implementación, o por la aparición de efectos colaterales inesperados e indeseados (Martínez-Abraín et al. 2004).

Los análisis de viabilidad poblacional

Una de las herramientas cuantitativas clave con las que cuenta la biología de la conservación son los análisis de viabilidad poblacional (PVA) (Beissinger & Westphal 1998, Noss 1999, Beissinger & McCullough 2002, Morris & Doak 2002). Se trata de herramientas de modelización predictivas desarrolladas para: a) predecir el tamaño futuro de una población; b) establecer la probabilidad de extinción de una población en un tiempo determinado; c) determinar qué estrategias de manejo o conservación maximizarían las probabilidades de persistencia de una población; d) y explorar las consecuencias de distintas asunciones teóricas en la dinámica de poblaciones con fines de conservación o de explotación de poblaciones (Tuljapurkar & Caswell 1997, Coulson et al. 2001, Caswell 2001). Este tipo de análisis parte de datos de tamaño

poblacional y/o parámetros demográficos que posteriormente son utilizados para proyectar el tamaño y estructura futura de las poblaciones (Caswell 2001). Sin embargo, es importante resaltar que su fiabilidad no es absoluta y presentan importantes limitaciones (Coulson et al. 2001). Una de las mayores limitaciones que los modelos de poblaciones presentan a la hora de aplicarlos a la conservación es la falta de datos de calidad que reflejen la distribución en el tiempo y en el espacio de las poblaciones, y permitan estimar cuáles son los valores de los parámetros demográficos (incluyendo sus varianzas) para gran cantidad de taxones de interés (Coulson et al. 2001, Beissinger & McCullough 2002, Williams et al. 2002, Frederiksen et al. 2005). Por lo tanto, los estudios individuales a largo plazo se hacen indispensables, especialmente en especies longevas o en aquellas especies que habitan en ambientes con elevada estocásticidad (Nations & Boyce 1997, Oro et al. 2004b).

Los análisis de perturbación son una de las principales aplicaciones de los modelos poblacionales a la conservación (Coulson et al. 2001); ya que indican cómo poder optimizar las estrategias de conservación, es decir, detectan cuáles son los parámetros demográficos con el mayor impacto potencial en la tasa de crecimiento de poblaciones (Caswell 1978, de Kroon et al. 1986, Tuljapurkar & Caswell 1997). Sin embargo, hay que tener en cuenta que algunos parámetros demográficos con gran impacto en la dinámica de las poblaciones pueden ser poco variables o difíciles de manipular (Goodman 1980).

Generalmente, la supervivencia adulta es el parámetro más importante en especies longevas con bajas tasas reproductivas (Saether & Bakke 2000). Para estas especies, una inversión de tiempo y recursos destinados a maximizar el éxito reproductor podría no ser la mejor estrategia, ya que su repercusión en las poblaciones sería mínima. Por el contrario, para especies con tasas de supervivencia bajas y alta fecundidad, tanto sus tasas de crecimiento poblacional como las probabilidades de extinción son especialmente sensibles a cambios en la supervivencia juvenil (Emlen & Pikitch 1989) y fecundidad (Saether & Bakke 2000). En algunos casos, la persistencia de una población o metapoblación va a depender en mayor medida de parámetros de dispersión que de parámetros reproductivos o de la supervivencia (Croxall & Rothery 1991, Oro 2003, Soutullo et al. 2008), e incluso de interacciones

con otras especies (Carrete et al. 2005). Varios estudios han evidenciado que los fenómenos de dispersión entre subpoblaciones tienden a reducir las probabilidades de extinción e incrementar la persistencia en el tiempo de la metapoblación (Burkey 1989).

En resumen, es de suma importancia conocer el valor y la variabilidad que presentan los distintos parámetros demográficos tanto espacial como temporalmente para poder generar predicciones precisas que permitan implementar acciones de manejo y conservación de especies o poblaciones amenazadas. En ultimo término deberían efectuarse estudios encaminados a investigar la efectividad de las acciones de conservación (Stem et al. 2005) que permitan basar el manejo de poblaciones en evidencias empíricas (Pullin 2004). Dichos estudios son especialmente relevantes para los gestores de la naturaleza, aunque todavía representan una minoría de las publicaciones científicas en revistas de conservación (Fazey et al. 2005).

AVES MARINAS Y CONSERVACIÓN

No todas las especies son igualmente vulnerables a la extinción; las especies especialmente susceptibles son aquellas con tamaño corporal grande, requerimientos de nicho especializados, posiciones elevadas en la cadena trófica, baja fecundidad, incapacidad de dispersión efectiva, migraciones estacionales, áreas de campeo extensas, distribución geográfica reducida, limitado número de poblaciones, tamaños poblacionales pequeños, densidades poblacionales bajas o escasa variabilidad genética (Primack 1995).

Las aves marinas son uno de los grupos donde su grado de amenaza se ha incrementado considerablemente durante las últimas décadas (Butchart et al. 2004). Las aves marinas son un grupo de organismos muy diverso adaptado a la vida en el medio marino, de donde mayoritariamente obtienen sus recursos y en donde pasan más del 90% de su tiempo de vida y dos terceras partes de su ciclo anual (Furness y Camphuysen 1997, Heppel et al. 2005). Una gran cantidad de especies visitan tierra firme únicamente para reproducirse, generalmente en la costa de islas y continentes

(Shreiber & Burger 2002). En su mayor parte son especies coloniales, monógamas y filopátricas al lugar de reproducción (Shreiber & Burger 2002). Son también animales longevos, cuyas tasas de supervivencia adulta se sitúan en torno al 90% en muchas especies (Shreiber and Burger 2002, Weimerskirch 2002), con bajas tasas de reproducción y unos tiempos de maduración sexual relativamente largos (Weimerskirch 2002). Sus rasgos historia de vida las convierten en organismos vulnerables a la reducción de sus densidades poblacionales o de la supervivencia adulta, al no poder responder de forma rápida a los cambios, debido a sus altos tiempos de generación (Croxall & Rothery 1991, Musick 1999).

Como especies depredadoras apicales de la cadena trófica sus poblaciones tienden a reflejar las condiciones del medio a grandes escalas tanto espaciales como temporales (Krebs 2001), convirtiéndolas en buenos "bioindicadores" o "biomonitores" de cambios ambientales (Croxall & Rothery 1991, Furness & Camphuysen 1997). Además, su naturaleza colonial facilita el seguimiento de sus densidades poblacionales y/o parámetros demográficos. Su dieta, condición física y parámetros demográficos pueden estar influenciados por cambios climáticos (Sydeman et al. 2001, Sandvik et al. 2005, Crespin et al. 2006, Lee et al. 2007), reflejar el estado de niveles inferiores de la cadena trófica como es el caso de algunas pesquerías (Frederiksen et al. 2004, Votier et al. 2004b, Velarde et al. 2004, Phillips et al. 2006), e indicar niveles de contaminación marina (Arcos et al. 2002, Peterson et al. 2003, Velando et al. 2005, Martinez-Abrain et al. 2006, Perez et al. 2008).

En la actualidad, numerosas especies de aves marinas se encuentran amenazadas como consecuencia del impacto de algunas actividades antropogénicas. Las actividades humanas, directa o indirectamente, han provocando importantes cambios en sus parámetros demográficos (como la supervivencia, el reclutamiento o la reproducción) que han repercutido en la densidad de sus poblaciones y en la estructura de sus comunidades (Montevecchi 2002, Oro 1996, Furness 2003, Lewison et al. 2004, Votier et al. 2004b, Arcos et al. 2006, Votier et al. 2008). Las actividades antropogénicas con mayor impacto en las poblaciones de aves marinas pueden clasificarse en:

a) molestias o <u>modificación directa del hábitat de cría</u> (Burger y Gochfeld 1993, Burger & Gochfeld 1994, Boersma et al. 2002, Beale & Monaghan 2004).

b) <u>explotación humana directa</u> para alimento, plumas ornamentales y aceite, (Burger & Gochfeld 1994, Boersma et al. 2002).

c) <u>introducción de especies exóticas</u> que compiten por espacio (Williamson 1996); de especies depredadoras, principalmente pequeños mamíferos (Burger & Gochfeld 1994, Martin et al. 2000, Igual et al. 2007); o de especies que favorecen el incremento de las densidades de población de depredadores naturales resultando en una mayor depredación sobre las aves marinas, fenómeno conocido como hiperdepredación (Courchamp et al. 2000, Monleón et al. 2008).

d) <u>interacción con pesquerías</u>. La mortalidad en artes de pesca, principalmente en el palangre, es una de las mayores amenazas para las aves marinas de medio-gran tamaño (Brothers et al. 1999, Montevecchi 2002, Tuck et al. 2001, Cooper et al. 2003, Lewison et al. 2004, Arcos et al. 2006). Al mismo tiempo, la sobreexplotación de los recursos marinos por las pesquerías conlleva una reducción en la abundancia y disponibilidad de las presas para las aves marinas, que afecta a la dinámica de sus poblaciones principalmente a través de efectos en su éxito reproductor (Montevecchi 2002, Jackson et al. 2001, Furness 2003). El aporte extra de alimentos procedentes de descartes pesqueros, del cual se aprovechan especialmente las especies más oportunistas, puede afectar a sus parámetros demográficos (incrementando el éxito reproductor e incluso la supervivencia), al tamaño de sus poblaciones (incrementando sus densidades) y a la estructura de la comunidad (Oro et al. 1995, Garthe et al. 1996, Oro 1996, Furness 1999, Oro 1999, Oro & Furness 2002, Tasker et al. 2000, Arcos 2001, Furness 2003, Oro et al. 2004a, Votier et al. 2004b).

e) <u>contaminación</u> (ver revisión en Nisbet 1994, Burger & Gochfeld 2002). La contaminación en aves marinas puede tener efectos directos a corto plazo sobre su supervivencia y reproducción, como sería el caso de las afecciones de vertidos de hidrocarburos e incluso la ingesta de plásticos (Ryan 1987, Kinan & Coulsins 2000, Wiese et al. 2001, Salomone 2002, Peterson et al. 2003, Heubeck et al. 2003, Martínez-Abraín et al. 2006), o puede tener efectos difusos a largo plazo por bioacumulación de metales pesados y organoclorados incorporados a través de la dieta e ingestión de plásticos (Ryan et al. 1988, Vlietstra et al. 2002).

EL PAÍÑO EUROPEO (*Hydrobates pelagicus*) COMO CASO DE ESTUDIO

El orden de los Procellariiformes (albatros, pardelas y petreles), con un 45% de sus especies representantes catalogadas en peligro (IUCN-Red List 2007), es uno de los grupos de aves marinas más vulnerable a las amenazas de origen antrópico. Se trata de aves marinas "extremas", donde todas las especies presentan una supervivencia extremadamente alta, una fecundidad extremadamente baja, una gran filopatria al lugar de cría (que en un 75 % de las especies se sitúa en cavidades) y una dependencia total a los recursos marinos (Warham 1990, Warham 1996, Schreiber & Burger, 2001).

El paíño europeo (*Hydrobates pelagicus*) es un ave marina perteneciente al Orden Procellariiformes (Fig. 1.). Al igual que todas las especies pertenecientes a este Orden es una ave pelágica que presenta una gran longevidad (se ha recapturado un ave con 32 años, European Longevity Records, Euring), una baja fecundidad y unos periodos de incubación y cuidado de la progenie largos (Warham 1990). Con un peso medio de 28 gramos, una longitud de 15 cm y una envergadura de 36 cm es el petrel más pequeño del Paleártico (Cramp & Simmons 1977).

FIGURA 1. Paíño europeo, *Hydrobates pelagicus.*

<div align="center">Distribución y ecología</div>

El paíño europeo es la única especie descrita dentro del género *Hydrobates*. Sin embargo, se han diferenciado dos subespecies (Cagnon et al. 2004): *H. pelagicus pelagicus* (Linnaeus, 1758) que se localiza a lo largo de la costa Europea Atlántica, y la subespecie *H. pelagicus melitensis* (Schembri, 1843) en el mar Mediterráneo (Fig. 2). Es una especie común a lo largo de la costa atlántica, pero la subespecie mediterránea ha sufrido un acentuado declive debido al resultado de la actividad turística y la introducción de depredadores en la islas (Martin et al. 2000, Mínguez et al. 2003). En el Libro Rojo de las Aves de España la especie se clasifica como "Vulnerable" (Mínguez 2004) y según el Real Decreto 439/1990 que regula el Catálogo Nacional de Especies Amenazadas, está considerada "De interés especial".
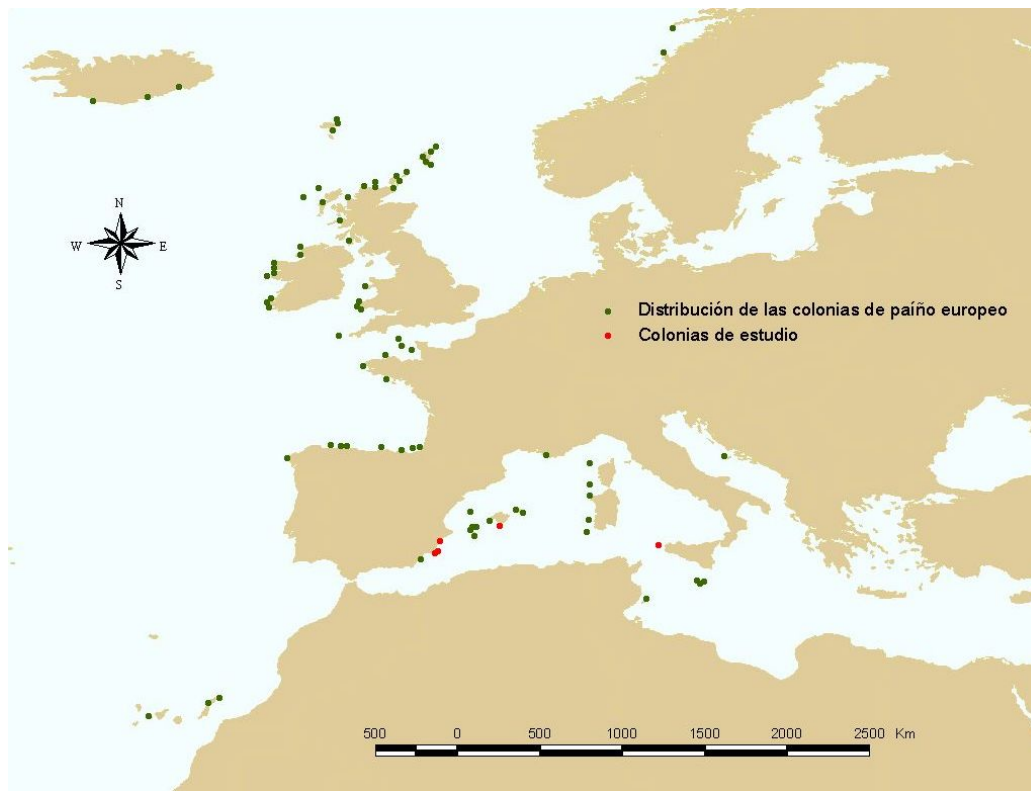

FIGURA 2. Localización de las colonias conocidas de paíño europeo (*Hydrobates pelagicus*).

El paíño europeo únicamente visita tierra firme para reproducirse o en busca de una pareja y/o lugar apto para la cría (Warham 1990). En tierra presenta una actividad estrictamente nocturna, probablemente para evadir depredadores diurnos

como los láridos o las aves rapaces (Watanuki 1986, Warham 1990, Martínez-Abraín et al. 2005). De hecho, en noches con luna llena se observa una reducción en la actividad de individuos no-reproductores en tierra firme (Watanuki 1986, Mougeot & Bretagnolle 2000). La mayor parte de los individuos visitan tierra firme a partir de su segundo año de vida tras permanecer su primer año en mar abierto (Okill & Bolton 2005). Existe una gran cantidad de individuos jóvenes "no-reproductores" que visitan las diferentes colonias de cría de la especie por las noches (Scott 1970, Okill & Bolton 2005). La edad de estos individuos únicamente puede ser determinada tras su marcaje como pollos, puesto que no existen diferencias de plumaje que permitan conocer la edad de esta especie una vez adquiere el plumaje adulto; a partir de su segundo año (Scott 1970).

Sus colonias de cría pueden albergar desde unos pocos individuos (p.e. Islas Columbretes, Castellón, España; obs. pers.) a cientos (p.e. Isla de Benidorm, Alicante, España; Mínguez 1994) o miles de parejas (p.e. Isla de Marettimo, Italia; Lo Valvo & Massa 2000). La mayoría de las colonias de cría se localizan en islas e islotes, siendo escasísimas las colonias encontradas en acantilados continentales (en la Península Ibérica tan sólo se ha localizado una en Cabo Ogoño, Bizkaia; Franco et al. 2004). Sus nidos se localizan en grietas, fisuras, pequeñas cavidades, cuevas, derrubios de piedras de tamaño medio y grande o bajo la vegetación (Scott 1970, Ramos et al. 1997, Ratcliffe et al. 1998b). La especie presenta una gran fidelidad a su nido y pareja (Warham 1990, Mínguez & Oro 2003). Mediante estudios de captura en redes se ha observado que los individuos reproductores rara vez son capturados a más de 200 metros de su nido (Scott 1970) y los cambios de colonia, aun incluso dentro de una misma isla, son muy poco frecuentes (Tavecchia et al. 2008).

En el área Mediterránea, los paíños comienzan a visitar sus colonias de cría a finales de marzo (Minguez 1994). El periodo de puesta se extiende durante unos 3 meses; las primeras puestas se producen a mediados de abril, la mayor parte se concentran entre mediados de mayo y mediados de junio, y las últimas se prolongan hasta la primera quincena de julio (Mínguez 1994). Se ha observado que las fechas medias y medianas de puesta, así como sus rangos varían en gran medida entre años (datos propios). En las colonias Atlánticas las fechas de puesta son más tardías que

en las colonias Mediterráneas, comenzando en mayo (Davis 1957, Mínguez et al. 1992). Parece ser que la temporada de reproducción de la especie se retrasa conforme las colonias se localizan en zonas más septentrionales (Davis 1957, Mínguez et al. 1992). La prospección de las colonias de cría por individuos jóvenes tiene lugar principalmente a finales de la estación reproductora, ya que de esta forma pueden obtener información local de la productividad o fertilidad de la colonia (*patch*); se trata pues de un mecanismo de selección de hábitat (Furness & Baillie 1981, Boulinier & Lemel 1996).

Al igual que todos los Procellariiformes, el paíño pone un único huevo de grandes dimensiones (6.77± 0.6 gramos; 23.5% con respecto al peso medio corporal de un adulto; Mínguez 1997). En ocasiones excepcionales, si la puesta fracasa al principio de la temporada de cría son capaces de reponerla (Mínguez 1997). El huevo es incubado por ambos sexos durante unos 40 días, en turnos de incubación medios de 2 días pero que pueden variar entre los 1 y 5 días (Scott 1970, Davis 1957, Mínguez 1998). Tras la eclosión del huevo los adultos permanecen durante todo el día en el nido durante la primera semana (Mínguez & Oro 2003). A partir de entonces, el pollo tan sólo es visitado por la noche por ambos progenitores, que le proporcionan el alimento. En torno a los 54 días de edad, los pollos alcanzan el 150% del peso de los adultos (Mínguez 1996). La frecuencia de las cebas va disminuyendo y en torno a los 63-70 días de vida los pollos abandonan las colonias (Davis 1957, Bolton 1995a, b, Mínguez 1996).

No se sabe con certeza si los individuos de las poblaciones mediterráneas abandonan este mar durante el invierno. Hashmi & Fliege (1994) estimaron una entrada en el Mediterráneo desde agosto a diciembre de unos 6300-9500 paíños y una salida hacia aguas atlánticas de unos 1100-1700, número muy inferior al de la población mediterránea. Los individuos de las poblaciones del Atlántico Norte se dirigen en otoño (septiembre-noviembre) hacia el sur, llegando a las costas meridionales del continente africano (Mainwood 1976).

Los paíños capturan su alimento picando rápidamente sobre la superficie del agua, ayudándose a veces con sus patas (Warham 1990, Warham 1996). El gran desarrollo

del sentido del olfato en esta especie (De León et al. 2003) podría estar implicado en la búsqueda de alimento, como se ha demostrado en otras especies de petreles (Warham 1990, Warham 1996, Nevitt 2000). Su dieta durante el periodo reproductor se compone principalmente de organismos oceánicos y neríticos: ictioplancton (*Gadidae, Ammodytidae, Myctophidae*); microzooplancton (*Copepoda, Euphausiacea, Chaetognatha, Anthomedusae,* y larvas meroplanctónicas); y especies bioluminiscentes que migran desde aguas profundas a la superficie por la noche (D'Elbee & Hemery 1998). El segundo grupo de organismos presentes en su dieta son organismos litorales (*Gobiidae*) e intersticiales suprabénticos (principalmente isópodos *Cirolanidae*) (D'Elbee & Hemery 1998).

Parámetros demográficos

En algunas colonias atlánticas se ha descrito intermitencia facultativa en la reproducción, es decir, la existencia de años sabáticos entre temporadas reproductoras (Hémery et al. 1986). El éxito reproductor de la especie muestra variaciones interanuales y espaciales (Moreno et al. 2003, Mínguez & Oro 2003, Tavecchia et al. 2008). Estas se deben principalmente a variaciones en el éxito de eclosión, siendo el éxito de emplumamiento generalmente elevado y más uniforme entre años (Mínguez & Oro 2003). En nidos naturales, los huevos pueden ser dañados por pequeñas piedras que se desprendan o se encuentren en la superficie del nido (Bolton et al. 2004). Este hecho, unido a la reducción en las interferencias como las peleas territoriales entre individuos en la colonias, hace que el éxito reproductor de los individuos que crían en nidales artificiales sea generalmente superior (de León & Minguez 2003, Bolton et al. 2004). De León & Mínguez (2003) estimaron un éxito del paíño en una colonia de la isla de Benidorm (denominada colonia 2) durante el perido 1997-2001 de 0.50 (±0.29 ES) en nidos naturales y 0.77 (±0.22 ES) en cajas nido. Tavecchia y colaboradores (2008) estimaron un éxito reproductor medio durante el periodo 1993-2002 de 0.49 y 0.51 en las colonias 1 y 2 de la isla de Benidorm, respectivamente. Las diferencias interanuales observadas en la supervivencia de los pollos sugieren que la cantidad de cuidado parental, en términos de alimentación y aporte de calor, podría estar condicionada por la disponibilidad de alimento tras la eclosión (Mínguez & Oro 2003). Las interacciones con otras especies

de aves, como las gaviotas o los cormoranes, pueden afectar a su éxito reproductor, tanto por depredación directa de adultos o de pollos (Oro et al. 2005), como por destrucción de su hábitat de cría (Bernard Cadiou, com. pers).

La supervivencia adulta de los individuos reproductores es variable tanto a nivel espacial como temporal (Oro et al. 2005, Tavecchia et al. 2008) y puede verse afectada por la depredación de láridos (Oro et al. 2005). Oro y colaboradores (2005) estimaron que la supervivencia del paíño durante el periodo 1993- 2003 en la colonia 1 de la isla de Benidorm varió entre 0.70 y 0.95 y mostró un valor medio de 0.83. Tavecchia et al. (2008), para periodo 1993-2002, estimaron una supervivencia media de 0.781 ($\pm$0.019 SE) y 0.690 ($\pm$0.036 SE) en la colonias 1 y 2 de la isla de Benidorm, respectivamente.

Problemas de conservación

A la hora de evaluar el estado de conservación de la especie es necesario disponer de estimas fiables de la evolución temporal de sus tamaños poblacionales o de sus parámetros demográficos (Russell 1999, Caswell 2001, Oro et al. 2004b, Tavecchia et al. 2008). El censo de las poblaciones reproductoras de paíño europeo es especialmente complejo debido a la inaccesibilidad de sus lugares de nidificación y la dificultad de distinción de los individuos no-reproductores de los reproductores en el entorno de las colonias de cría (Furness & Baillie 1981, Ambagis 2004, Mitchell & Newton 2000). La estima más reciente de la población europea oscila entre 430.000 y 510.000 parejas reproductoras (BirdLife International 2004) y la población española se estima entre las 5.000 y 10.000 parejas reproductoras (Mínguez 2004). Ambas son estimas poco precisas, por lo que es necesario contar con mecanismos que permitan evaluar la evolución de sus poblaciones en el tiempo. Como especie longeva, la supervivencia adulta es el parámetro demográfico que más afecta a la tasa de crecimiento poblacional (Saether & Bakke 2000). Por tanto, la identificación de los factores que incrementen la mortalidad adulta y el diseño e implementación de medidas correctoras efectivas deben ser actuaciones prioritarias en las estrategias y programas de conservación para garantizar la viabilidad de sus poblaciones.

La modificación del hábitat y la introducción las especies exóticas son las mayores amenazas para el paíño europeo en sus colonias de cría (Mínguez et al. 2003, Martin et al. 2000, de León et al. 2006). La distribución actual de sus colonias se limita a islas e islotes libres de depredadores mamíferos, como las ratas (Martin et al. 2000, de León et al. 2006). La presencia de ratas en colonias de cría de procellariiformes afecta principalmente a su productividad, al depredar huevos y/o pollos (Igual et al. 2006). Sin embargo, a diferencia de otras especies de mayor tamaño, las ratas depredan también sobre paíños adultos, afectando a su supervivencia e impidiendo que puedan coexistir en un mismo lugar (Atkinson 1985, Martin et al. 2000). La depredación que diversas especies de láridos como la gaviota patiamarilla (*Larus michahellis*) o la gaviota sombría (*Larus fuscus*) ejercen sobre adultos y pollos de paíño europeo en sus colonias de cría es otra de las principales amenazas para la especie (Fig 3) (Oro et al. 2005). Se ha observado que, a menudo, esta causa de mortalidad en la especie se debe a una depredación por parte de individuos especialistas (Oro et al. 2005).

FIGURA 3. Egagrópila de gaviota patiamarilla (*Larus michahellis*) con restos de un paíño europeo (*Hydrobates pelagicus*) depredado.

En el mar, la disponibilidad de alimento y la contaminación son los aspectos más relevantes para su conservación (Hemery 1986, Mínguez et al. 2003, Azkona et al. 2006). En algunas poblaciones atlánticas se ha observado que la intermitencia en la reproducción y la productividad de las colonias podrían estar ligadas a la

disponibilidad de presas durante la época reproductora (Hemery 1986). La contaminación por vertidos de crudo puede afectar a la especie directamente, siendo una causa de mortalidad, o indirectamente, a través de la degradación del medio marino o la afección a especies presa (Azkona et al. 2006). Otro tipo de contaminación con efectos indeseados para el paíño es la contaminación lumínica. Como sucede con otras especies de Procellariiformes, los individuos jóvenes, al abandonar las colonias pueden desorientarse y ser atraídos por las luces de las ciudades (Le Corre et al. 2002). Además la contaminación lumínica en zonas de cría podría incrementar la depredación por parte de especies diurnas como los láridos (Oro et al. 2005). A diferencia de otras especies de aves marinas y debido a su pequeño tamaño, el paíño europeo no es susceptible de ser capturado incidentalmente en artes de pesca como el palangre.

ENFOQUE DE LA TESIS

Esta tesis doctoral se ha centrado en el estudio de los rasgos de vida evolutivos y en la diagnosis de conservación de poblaciones de paíño europeo (*Hydrobates pelagicus melitensis*) con el objectivo de i) proporcionar información sobre las tácticas de historias de vida de los individuos, ii) explorar los mecanismos responsables de la variabilidad espacio-temporal de las poblaciones Mediterráneas y iii) verificar la eficacia de medidas concretas de conservación. Para el desarrollo de la tesis se han recopilado datos de seguimiento individual a medio-largo plazo de paíño europeo en seis colonias reproductoras localizadas en 5 islas mediterráneas (Fig. 2): Benidorm (Alicante-España), Hormigas (Murcia-España), Palomas (Murcia-España), Na Plana (Cabrera, Baleares-España) y Marettimo (Sicilia-Italia). Mi trabajo de campo (2003-2008) se ha centrado en las dos colonias reproductoras de paíño localizadas en la isla de Benidorm, donde he continuado el seguimiento individualizado de aves reproductoras, su descendencia y sus nidos, que comenzó en el año 1993. Estas dos colonias han sido objeto de numerosos estudios científicos desde el comienzo de su seguimiento, lo que ha permitido basar en resultados previos parte de los trabajos llevados a cabo.

Esta tesis doctoral está dividida en cuatro capítulos que integran enfoques metodológicos, demográficos, evolutivos y de manejo aplicado a la conservación (Fig 4).
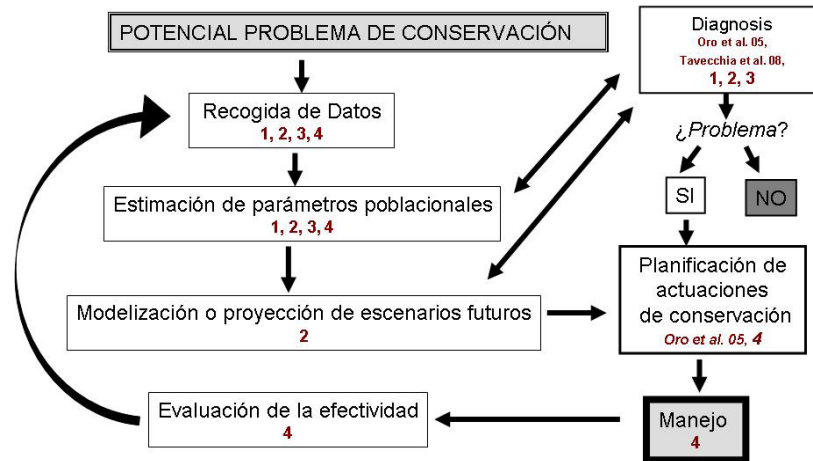

FIGURA 4. Esquema del proceso de trabajo seguido en el trascurso de la tesis. Los números en la figura hacen referencia al capítulo en el que se trata cada aspecto.

En el estudio de dinámica de poblaciones, evolución de rasgos historias de vida o para hacer diagnosis en conservación, la obtención de buenos datos que se deriven en estimas robustas de parámetros demográficos y/o de tamaños poblacionales es el punto de partida fundamental. El primer capítulo (**Capítulo 1**) se centra en la evaluación de los aspectos metodológicos de seguimiento individual comúnmente utilizados para el monitoreo de poblaciones y obtención de estimas de parámetros demográficos de paíño europeo y otras especies con hábitats de cría similares, como petreles y pardelas. Concretamente se han evaluado las ventajas y desventajas del método de captura directa de aves en sus nidos frente a la captura mediante redes instaladas en los alrededores de las colonias de cría (con o sin reclamos) para obtener estimas robustas de tamaño poblacional y supervivencia, usando los datos de monitoreo de seis poblaciones mediterráneas de paíño europeo. La supervivencia adulta es habitualmente el parámetro clave para la conservación de especies longevas. Las estimas de supervivencia obtenidas para las seis poblaciones estudiadas nos dan una visión a gran escala de los valores que adquiere dicho parámetro a una gran escala espacio-temporal. En este sentido, el estudio de la variabilidad o sincronización espacio-temporal de los rasgos de vida es esencial para comprender la influencia de factores ecológicos y/o evolutivos de los que va a depender la

conservación de poblaciones. Sin embargo, las poblaciones de especies longevas son generalmente conjuntos heterogéneos de individuos, entre los que factores como la edad o la experiencia reproductora pueden afectar a sus parámetros demográficos. Desde un punto de vista evolutivo, la teoría de historias de vida predice que mayores inversiones de esfuerzo en la reproducción deberían acarrear mayores costes, que podrían expresarse en una reducción de la supervivencia o productividad, especialmente entre los individuos jóvenes e inexpertos, que no siempre podrían optimizar su inversión en la reproducción. Por ello, en el **Capítulo 2** se ha estudiado como varían la supervivencia, el reclutamiento y el éxito reproductor en función de la edad a diferentes escalas espaciales: a pequeña escala (entre las dos colonias situadas en la isla de Benidorm) y a gran escala (entre las colonias de Benidorm y la de Marettimo en Italia). Las estimas edad- y colonia-dependientes de los parámetros demográficos obtenidas han sido incorporadas mediante modelos matriciales estructurados de poblaciones para calcular la tasa de crecimiento poblacional esperada. Estos modelos han permitido determinar la contribución de cada uno de los parámetros demográficos estimados a la tasa de crecimiento poblacional esperada y, por tanto, recomendar cuales deberían ser los parámetros clave sobre los que encaminar las medidas de conservación para la especie. En el **Capítulo 3** se han analizado los compromisos entre reproducción y supervivencia en función de la experiencia reproductora. En concreto se estudió como la experiencia reproductora y la inversión actual en la reproducción se asociaban a la expresión de un coste de la reproducción en términos de reducción de la supervivencia y/o del éxito reproductor futuro. Finalmente, en el **Capítulo 4** se ha evaluado la eficacia de un programa de descaste selectivo de gaviotas patiamarillas (*Larus michahellis*) especialistas en base a evidencias previas que indicaron la potencial afección de estos depredadores sobre la supervivencia adulta del paíño, parámetro clave para la persistencia de sus poblaciones. La eliminación selectiva de depredadores ha permitido estimar el efecto de la depredación tanto en la supervivencia adulta como en el éxito reproductor mediante la comparación de las estimas de ambos parámetros antes y después de que las acciones de manejo se llevaran a cabo. Además, se realizan recomendaciones para el manejo de depredadores facultativos especialistas que generen problemas de conservación en especies-presa secundarias.

CAPÍTULO 1

RECAPTURE PROCESSES AND BIOLOGICAL INFERENCE IN MONITORING BURROWING NESTING SEABIRDS

Recapture processes and biological inference in monitoring burrowing nesting seabirds

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(**Population Ecology**, *in revision*).

ABSTRACT

Capture-mark-recapture methods are widely used for diagnosis and management of natural populations as they permit to obtain robust estimate of population abundance and demographic parameters from incomplete records of individual life-histories. The statistical analyses of capture-recapture data, however, relay on the assumption of equal parameters across individuals. Using data from six medium-to-long term monitoring schemes of Mediterranean populations of the European storm petrel *Hydrobates pelagicus*, we empirically showed that the level of heterogeneity across individual and the consequent bias on the parameter of interest depends on the recapture methodology with important consequences for experimental design. We found that the recapture probability varied over time and among methodologies but that the estimate of survival probability of resident birds was fairly similar across the studies. The differences found in survival seemed to depend on biological variability between sites, i.e. predation pressure, and not of recapture methods. However, capture methodology had a strong influence on the actual proportion of transients, i.e. individuals never caught after marking, and ultimately on the estimate of population size and its reliability.

Keywords: capture-recapture analysis; monitoring scheme; population size; Procellariiformes; survival probability; transient.

INTRODUCTION

Medium to long-term monitoring schemes aim to provide valuable information on demographic parameters for species, or population, diagnosis (Spina et al. 1993, Gregory et al. 2005, Nichols & Williams 2006). In natural populations accurate estimates of these parameters are difficult to obtain due to sampling errors in counts and incomplete data on individual life-histories (Williams et al. 2002, Sutherland 2006). Consequently, the most common methods to estimate population parameters

are based on a statistical framework that accommodates a detection failure, e.g. 'distance-sampling' (Buckland et al. 1993) or 'capture-mark-recapture' techniques (Seber 1962, Williams et al. 2002). In capture-mark-recapture methods, the recapture probability, e.g. the probability to capture or detect an individual known to be in the population, is often considered a nuisance parameter that must be estimated only to obtain unbiased measured of survival probability or population abundance. However, variations and heterogeneity in the recapture probability reflect changes in sampling effort as well as real biological processes (Clobert et al. 1994, Viallefont et al. 1995, Crespin et al. 2008). In addition, recapture processes might be more complex than expected (Pradel et al. 1997, Crespin et al. 2008) and undetected sources of variation in the probability of recapture may still lead to biased estimate of survival or animal abundance (Pledger & Efford 1998, Kendall 1999, Kendall et al. 2004). As different field protocols might lead to different types of biases it is important to evaluate which method is more appropriate for the estimate of the parameter of interest.

Using data from six different medium-long term monitoring projects we investigated the effects of sampling effort and sampling methodology for demographic inferences on a burrowing nesting bird, the European storm petrel *Hydrobates pelagicus melitensis*. The European storm petrel is a vulnerable small seabird (average body mass 28 g, Warham 1990) of the Mediterranean basin. The specie is nowadays confined to islets, following the introduction of predators on large islands with human colonisation (Thibault et al. 1996, Martin et al. 2000, de León et al. 2006). Storm petrels are pelagic and return to land at night only to breed or to prospect potential breeding colonies (Watanuki 1986, Warham 1990). The activity pattern coupled with the burrowing nesting habit of the species (Scott 1970, Ramos et al. 1997, Ratcliffe et al. 1998b) makes its populations difficult to monitor through classical nest counts (Mitchell & Newton 2000). Exhaustive counts of breeding birds or burrows are in most cases impossible and estimates of population size of this species typically range widely even for a single colony (Ambagis 2004 and references therein). The same problem affects species with similar life histories and breeding habits such as other petrels and shearwaters. Consequently, insights in their population dynamics can be better achieved through the analysis of life-histories of individually marked birds (Oro et al. 2004b, Tavecchia et al. 2008, Sanz-Aguilar et al.

2008, Sanz-Aguilar et al. 2009b). Individual-based data are typically collected by capturing incubating birds at their nests or using mist-nests placed near the breeding colonies (Hemery1980, Furness & Baillie 1981, Sydeman et al. 1998, Amengual et al. 1999, Lo Valvo & Massa 2000, Sanz-Aguilar et al. 2008). These data can be used to estimate several demographic parameters providing that some critical assumptions are not violated (Seber 1962, Lebreton et al. 1992). For example, estimates of population abundance derived from Jolly-Seber models for open populations (Seber 1962) are biased if individuals do not have the same detectability and/or survival (Link 2004, Schwarz & Arnason 2006).

In order to investigate the potential and limitations of alternative protocols we i) gathered capture-recapture data from six storm petrel breeding locations in the Mediterranean basin and verify whether they met the basic assumptions of capture-recapture analysis, ii) modelled recapture processes, ii) estimated annual survival probability, estimated the proportion of transient birds and the population size and iii) evaluated differences between colonies in relation to monitoring protocols.
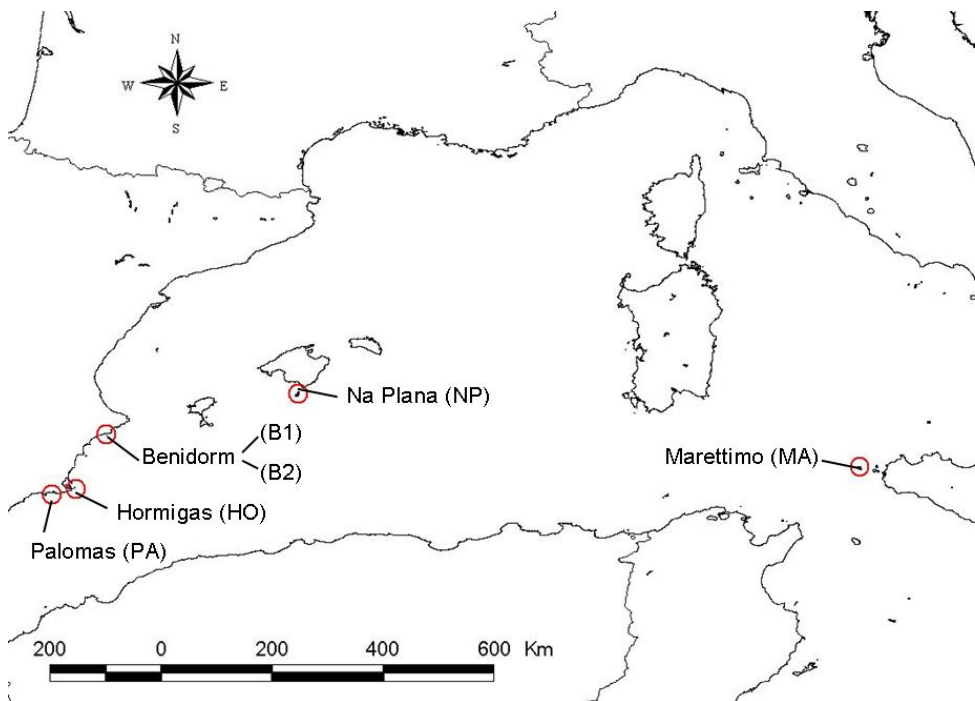

FIGURE 1. Location of the study areas: caves 1 (B1) and 2 (B2) in Benidorm Island (Alicante, Spain), Marettimo Island (MA) (Italy), Hormigas Island (HO) and Palomas Island (PA) (Murcia, Spain), and Na Plana Island (NP) (Cabrera Archipelago, Mallorca, Spain).

TABLE 1. Characteristics of storm petrel monitoring schemes at five islands of the Mediterranean basin.

Colony - notation- area (ha)	Years of monitoring	Methodology	Birds' breeding state
Benidorm (Alicante, Spain) - B1 - 6.5	1993-2006	Nest monitoring	Breeders
Benidorm (Alicante, Spain) - B2 - 6.5	1994-2006	Nest monitoring	Breeders
Marettimo (Sicily, Italy) - MA - 1200	1991-1994 ; 1996 ; 1998-2006	Nest monitoring	Breeders
Hormigas (Murcia, Spain) - HO - 0.7	1996-1997 ; 1999-2000 ; 2004-2006	Mist-netting	Unknown
Palomas (Murcia, Spain) - PA - 1.2	1996-2000 ; 2004-2006	Mist-netting	Unknown
Na Plana (Cabrera, Spain) - NP - 5.6	1994-1998	Mist-netting + lures-lures	Unknown

TABLE 2. Testing assumptions of the Cormark-Jolly Seber model, including time- and colony-dependent parameters for birds at the colonies of Benidorm Island (noted B1 and B2, respectively), Marettimo (MA), Hormigas (HO), Palomas (PA), and Na Plana (NP). Significant chi-square statistics ($p<0.05$) are in bold.

Colony	B1		B2		MA		HO		PA		NP	
Goodness-of-fit components	$\chi2$	df	$\chi2$	df	$\chi2$	df	$\chi2$	df	$\chi2$	df	$\chi2$	df
'CJS Model'total	**85.16**	**43**	**57.25**	**38**	**101.64**	**68**	**28.71**	**10**	**48.18**	**16**	**26.51**	**6**
3.SR *transient effect*	**40.88**	**12**	**22.31**	**11**	**40.55**	**11**	**27.09**	**4**	**29.92**	**6**	**23.73**	**3**
3.SM	8.29	12	16.81	10	20.11	21	0.89	2	**12.36**	**3**	1.30	1
2.CT *trap-dependence effect*	**28.01**	**11**	10.59	10	**22.63**	**9**	0.73	2	5.43	4	1.48	2
2.CL	7.97	8	7.54	7	18.35	27	0.00	2	0.48	3	0.00	1
'Model with transients'	44.28	31	34.94	27	61.09	57	1.62	6	18.26	10	2.78	4
ĉ - 'Model with transients'	1.43		1.29		1.07		1		1.83		1	

METHODS

Individual data and monitoring schemes

We used information on five independent monitoring schemes of six storm petrel colonies at five islands of the Mediterranean basin (Fig. 1). All schemes aimed to collect data for population diagnosis and to provide information for management actions. Schemes, however, varied in length, methods and sample size according to the locations, number of people involved and financial support (Table 1, Appendix I). Due to differences in length size each dataset have been treated separately using the same analytical procedure. For the sake of simplicity, we shall refer to locations using abbreviations on their names. So that the two colonies at Benidorm Island (Spain) are denoted 'B1' and 'B2', respectively; the one at Marettimo Island (Italy), 'MA' and those of Hormigas, Palomas and Na Plana (Spain), 'HO', 'PA' and 'NP', respectively (Fig. 1). We outlined below the relevant features of the datasets and refer readers to Appendix I for a detailed description of each monitoring protocol. In the three populations located inside accessible caves, 'B1', B2, and 'MA', respectively, animals were captured on their nest during incubation or, when attending recently hatched chicks (Table 1). In addition, in colonies 'B1' and 'B2' nests were followed during the whole breeding season to estimate breeding success (Sanz-Aguilar et al. 2008). This has not been possible in colony 'MA' due to the difficult access of the colony (Sanz-Aguilar et al. 2009b). At the other locations ('HO', 'PA' and 'NP', respectively), petrels were caught at night using mist nets (Table 1). In colony 'NP' petrels were lured into nets using a playback of their vocalizations, a method commonly employed to increase the number of captures (Table 1). In summary, individual encounter histories came from six locations and birds were captured using one of three methods: on their nest (3 programs), on mist-nets (2 programs) and on mist-nets combined with acoustic lures to attract birds (1 program).

Statistical analysis

Individual data collected by all six monitoring programs were analysed using capture-recapture techniques to estimate local survival and recapture probabilities

(Lebreton et al. 1992), transient proportions (Pradel et al. 1997) and population size (Schwarz & Arnason 2006). Captures within the same breeding season were pooled together to obtain a single capture-recapture occasion per year. Although some birds were recaptured more than once within a recapture occasion or breeding season, data were too sparse to use a robust design approach that allows to analyze recaptures within occasions together with recaptures between occasions (Kendall and Nichols1995, Kendall et al.1997). For each dataset the capture-recapture analysis began with a goodness-of-fit of a model assuming a full time variation of recapture and survival parameters, the Cormark-Jolly-Seber model (CJS) (Lebreton et al. 1992). Under the assumption that individuals share the same parameters, i.e. the homogeneity assumption, the distribution of individual encounter histories can be written as a combination of the probability to survival the interval [i, i+1], i.e. the survival probability at i typically noted ϕ_i, and the probability that an individual known to be alive is caught, or seen, at i, i.e. the recapture probability, typically noted p_i. The goodness-of-fit test of the CJS model assesses whether data meet the homogeneity assumption regardless of individual past and present history. The goodness-of-fit test is based on specific contingency tables for each recapture occasion and has been calculated using program U-CARE 2.2.2 (Choquet et al. 2005). The program includes specific test for the presence of transient birds, i.e. birds seen only at marking, noted 'Test 3.SR', that compares whether the survival probability soon after marking differs from the subsequent ones (see Appendix I in Tavecchia et al. 2008). This effect can be accommodated by including specific parameters for the first survival after marking (Pradel et al. 1997). This survival is then a weighted average between the survival of transient (equal to zero by definition) and the survival of resident birds. Pradel et al. (1997) have shown that the proportion of transients, τ_t, in the population can be calculated as the relative difference between the survival during the first year after marking, here noted ϕ', and the subsequent ones, here noted ϕ, so that:

$$\tau_i = 1 - \frac{\phi'_i}{\phi_i}$$

Confidence intervals for τ were calculated using the Delta method (Morgan 2000). The goodness-of-fit test also includes a specific test, named 'Test 2.CT', to verify whether some birds are captured more than others (Pradel 1993). Additional lack of fit can be taken into account by scaling model deviances using a scale parameter, classically denoted $\hat{c}$, as typically done in logistic linear regressions (Crawley 1993), calculated as the goodness-of-fit statistic on its degree of freedom (Lebreton et al. 1992). We then modelled the effects of time, of transient birds, of the recapture effort (i.e. number of capture occasions per year) and their statistical interaction. Models were built and fit to the data using program M-SURGE (Choquet et al. 2004; Choquet et al. 2006). Model selection was based on the Akaike's Information Criterion adjusted for small sample size (c) and overdispersion (Q) calculated as

$$QAIC_c = \frac{dev}{\hat{c}} + 2*np$$

where *dev* represents the model deviance; $\hat{c}$ the variance inflation factor; and *np* the number of separately identifiable parameters in the model (Burnham and Anderson 2002). Additionally for each model *j*, we calculated the Akaike weights, w_j, as an index of its relative plausibility (Burnham & Anderson 2002). For each location, the time-dependent estimates were obtained by model averaging in which each model contributed to the final estimate according to its Akaike weight (Burnham & Anderson 2002). Average estimates of survival and transient probability in each colony were obtained from models without a time effect in survival, whereas if necessary this effect was kept in the recapture probability. Comparisons between average estimates were done by the mean of a Z-test (Zar 1984) as estimates across datasets were independent. Finally, we obtained an estimate of the population size using the procedure POPAN in program MARK1.4 (White & Burnham 1999). This procedure is suitable to obtain estimate of size in open populations from capture-recapture data (Schwarz & Arnason 2006). The method, however, does not allow heterogeneity in survival among individuals and by consequence estimates were obtained from model without a transient effect. Note that in colonies 'B1', 'B2' and 'MA' where birds were captured at their nests, the estimated population size refers to the number of birds breeding into accessible nests and it does not allow inference on the total population of birds.

RESULTS

As a general procedure, we began by modeling the probability of recapture by testing a full effect of time, a linear constraint or the influence of recapture effort. We then modeled survival probability as a function of time, age-after marking (i.e. the 'transient' effect), and their statistical interaction. Although we found interesting similarities across datasets, the models with the highest Akaike weights differed at each location due to site-specific selective pressures but also to the different sample size and the associated statistical power. Each model selection is fully described in Appendix II and the models with the highest Akaike weights are summarized in Table 3, here we will outline the most relevant differences or similarities.

TABLE 3. Summary of model selection (including models with the highest Akaike weights) on local survival (noted ϕ' and ϕ for transient and resident birds respectively) and recapture probabilities (noted p) based on capture-recapture data from European storm petrels at the colonies of Benidorm (noted B1 and B2, respectively), Marettimo (MA), Hormigas (HO), Palomas (PA), and Na Plana (NP). See more details in Table S2-1 Appendix S2. Notation: np, number of parameters in the model; Dev = deviance; QAICc= Akaike's information criterion adjusted for small sample size (c) and overdispersion (Q); ΔQAICc=the difference in QAICc between the current and the model with the lowest QAICc; w_i=Akaike weigths, 't'=time effect, 'T'=linear trend in time. Symbol '+' indicates parallel variation, i.e. additive effect. Symbol '+' indicates interaction terms.

Model-colony notation	recapture	survival	np	Dev	QAICc	ΔQAICc	w_i
4 -B1	p_t	$\phi'_t + \phi_t$	27	2741.32	1971.01	0	0.93
5 -B2	p_T	$\phi'_t + \phi_t$	15	889.33	719.41	0	0.50
5 -MA	p_t	$\phi'_t * \phi$	27	3518.88	3342.67	0	0.52
6 -HO	p_t	$\phi' * \phi_t$	14	1308.98	1336.98	0	0.70
7 -PA	p_t	$\phi' * \phi$	9	1381.20	772.75	0	0.81
7 -NP	p_t	$\phi' * \phi$	6	634.06	646.06	0	0.57

The goodness of fit test revealed a significant difference in survival between newly marked and resident birds in all datasets (Table 2). We also found a significant trap-dependence effect at colonies 'B1' and 'MA' but not in the others datasets (Table 2). We began by building models to accommodate the transient effect by including two apparent age classes in survival probabilities (Pradel et al. 1997). The remaining heterogeneity was accounted for by scaling model deviances using a variance

inflation factor, $\hat{c}$, specific for each data set (Table 2). This was also done for 'B1' and 'MA' because models including both, a trap-dependence effect and a transient effect, are parameter redundant. Recapture probabilities varied over time in all locations, but not as a function of the recapture effort (Appendix II). As expected, recapture probability was highest at colonies 'B1' and 'B2' where nests were monitored throughout the breeding season, but, despite a similar method, it was lower at 'MA' because the capture protocol was based on only one visit per season (Appendix II). The recapture probability using mist nets was high in 'HO', but low at the other two colonies ('PA' and 'NP'), even when animals were lured in using recorded calls (Appendix II). Similarly, survival probability generally varied over time for resident and/or transient birds, with the exception of birds at colonies 'PA' and 'NA' where it was constant (Table 3; Appendix II). We found that average estimates of resident survival probability of all colonies ranged between 0.7 and 0.9 (Fig. 2). The highest survival was found in colonies 'MA' and 'HO' whilst the lower values were found in colonies 'B1' and 'B2' (Fig. 2, Table 4).
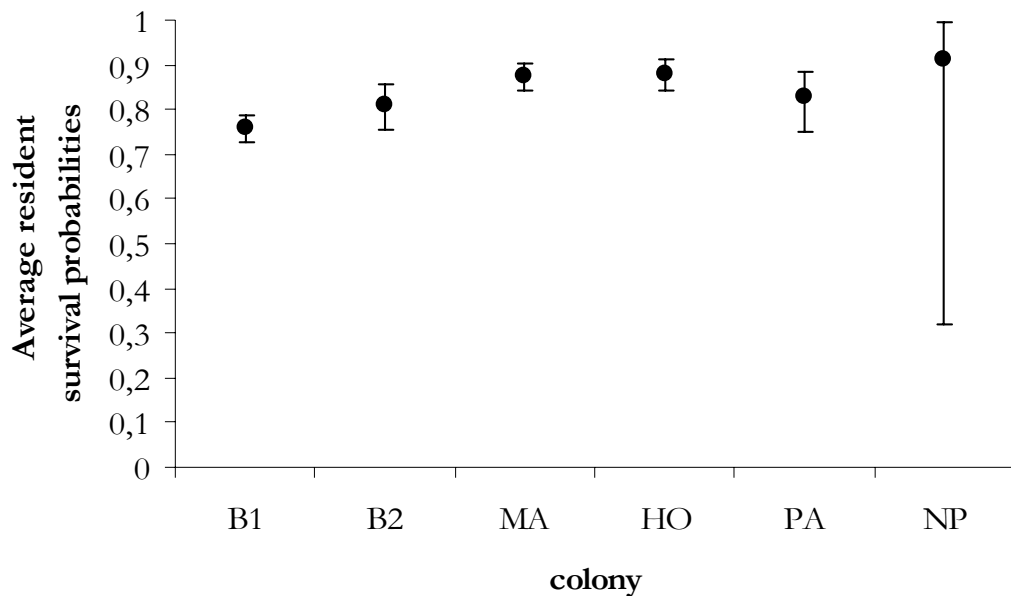

FIGURE 2. Average storm petrel resident survival probabilities during the study periods at colonies B1 and B2 (Benidorm), MA (Marettimo), HO (Hormigas), PA (Palomas), and NP (Na Plana) obtained from models (7-B1, 8-B2, 7-MA, 7-HO, 7-PA and 7-NP, Table A2-1 Appendix II).

TABLE 4. Z test comparison of average resident survival estimates and average transient proportions obtained from models (7-B1, 8-B2, 7-MA, 7-HO, 7-PA and 7-NP, Table A2-1 Appendix II) at colonies B1 and B2 (Benidorm), MA (Marettimo), HO (Hormigas), PA (Palomas), and NP (Na Plana). Significant effects (p<0.05) are in bold.

	Average resident survival probabilities					
	MA	B1	B2	PA	HO	NP
MA		**5.33**	**2.11**	1.32	0.27	0.04
B1	0.33		1.74	1.83	**5.25**	0.15
B2	0.30	1.14		0.35	**2.24**	0.10
PA	**2.78**	**4.32**	**3.23**		1.45	0.09
HO	0.10	1.96	0.19	**2.61**		0.03
NP	**5.23**	**8.64**	**6.24**	1.40	**5.29**	

(left vertical label: Average transient proportions)

Except at colony 'HO', the proportion of transients was higher in dataset from mist-net studies (Fig. 3, Table 4) with the highest value of 0.68 (SE: 0.06) at 'NP' where birds were captured using mist nets in combination with tape-lures (Fig. 3). This value however is not significantly different from the one at colony PA (Table 4).
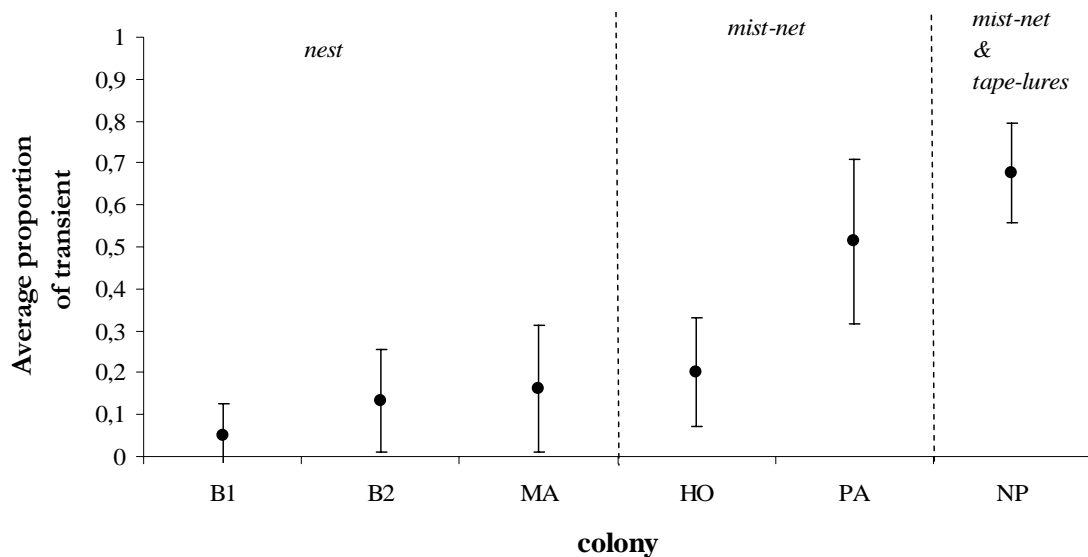

FIGURE 3. Estimated average proportion of transients in the studied colonies, noted B1 and B2 (Benidorm), MA (Marettimo), HO (Hormigas), PA (Palomas), and NP (Na Plana), obtained by models without time effects (Models 7-B1, 8-B2, 7-MA, 7HO, 7PA and 7-NP, Table A2-1 Appendix II).

For each colony, estimates of population sizes were obtained from the model with the highest Akaike weight without the transient effects (Appendix II). Population sizes at colonies 'B1', 'B2' and 'MA' well mirrored the number of birds present in monitored nests and ultimately the number of nests monitored (Appendix III). At colonies 'HO', 'PA' and 'NP', where petrels were captured using mist-nets, population estimates showed a great yearly variation and large confidence intervals, reflecting the uncertainty on the recapture probability (Appendix III).

DISCUSSION

Methods to obtain robust estimates of demographic parameters from individual-based data rely on the important assumption that all marked individuals should have the same survival and detection probabilities, the so called homogeneity assumption (Lebreton et al. 1992, Williams et al. 2002). In capture-mark-recapture studies, a given capture methodology might contribute to increase the level of heterogeneity across individuals with important consequences for the estimate of the parameter of interest.

Site- and method- specific differences in demographic parameters

A first result common to all datasets was that recapture probability was changing across studies and over time. Interestingly, this variability was not associated with the measure of the recapture effort, i.e. the number of days of capture per year. Recapture probability was generally higher when birds were captured on their nest but not in colony 'MA' due to the late time of the single visit. A late visit typically resulted in a low number of adult captured because adults tend to leave the nest few days after hatching (Mínguez & Oro 2003) but it allows to mark a high number of chicks (Lo Valvo & Massa 2000). In colonies where petrels were captured using mist-nets yearly variation in recapture probabilities may also respond to the seasonal change in the proportion of non-breeding prospectors, food availability, weather and the moon phase (Scot 1970, Furness & Baillie 1981, Watanuki 1986, Boulinier & Lemel 1996, Mougeot & Bretagnolle 2000). Bad and mild wind conditions can substantially alter mist net efficiency and therefore influence recapture probability if

the number of sessions per year is low, although recapture did not covary with the effort. An unexpected result was that recapture probability did not increase by using tape lures. This is probably because the majority of birds attracted by the playback are prospectors that are never captured again. So although the absolute number of birds captured with lures may be high, the number of recaptures is similar to the one obtained without lures.

A second interesting result common to all datasets was that a substantial proportion of birds captured were 'transient' individuals, i.e. individuals never seen again after marking (Pradel et al. 1997). The proportion of transient birds, however, was higher in datasets from mist net studies, and increased when birds were lured in the nets using a playback device suggesting that a high proportion of non-breeding prospectors may be prone to be captured with this method (Furness & Baillie 1981, Podolsky & Kress 1989). Okill & Bolton (2005) found that the prospector fraction of the storm petrel's population is composed by young birds aged between 2 to 5 and studies in other long-lived birds shown that survival probability is typically lower among the youngest age classes (Tavecchia et al. 2001, Ratcliffe et al. 2002). Consequently, studies in which a higher proportion of prospectors are captured should have a high level of heterogeneity in survival. Transient proportion, however, can also vary across studies despite a similar methodology due to site-specific differences in predation pressure, intrinsic individual quality (Tavecchia et al. 2008, Sanz-Aguilar et al. 2008), or colony attractiveness (Brown et al. 1990, Oro & Pradel 2000). We found, for example, that in the small islet of 'HO', the transient proportion was lower than the one found in the larger island of 'PA' despite birds were captured in mist-nests at both sites.

An important results was that average estimates of survival probability of resident birds, i.e. individuals that were recaptured at least once, appeared similar regardless the capture methodology or the site. An exception is Benidorm Island (colonies 'B1' and 'B2'), where predation by specialist yellow legged gulls *Larus michahellis* that breed inside the petrel colonies decreased survival of juvenile and adult petrels (Oro et al. 2005).

The presence of transients can be accommodated in models for the estimate of survival probability, but it can not in models for the estimate of population size where individual heterogeneity in survival and/or recapture impairs such estimate (Kendall et al. 2004). As a consequence, population numbers estimated from mist-nets studies, in which transient proportion is generally higher and recapture probability low, showed high confidence intervals and large variations in population numbers among years. In same cases, the population of resident birds can be estimated by correcting the estimate of population abundance by the transient proportion. However the obtained number might not be informative because only a small portion of the real population of breeders generally might be caught on nets, due to the difficulties to cover with nets the whole colonies areas. In the long-term monitoring studies in which individuals were caught in their nests we found heterogeneity in recapture probability, an effect noted as trap-dependence. This is probably due to the fact that some breeders are more easily captured than others depending on their nest location or accessibility (Crespin et al. 2008). As for the transient probability, this effect does not affect the probability of survival providing it is correctly included in the model (Prevot-Julliard et al. 1998). However it impairs once again a reliable estimation of population size. Pledger & Efford (1998) proposed a method to obtain unbiased estimate of population size including the form of recapture heterogeneity into the capture-recapture models, but Link (2003) has recently demonstrated that difficulties persisted. Note that in nest monitoring studies solving the heterogeneity problems does solve the puzzle because the population size estimated reflects the number of breeders present in monitored nests and not the absolute number of breeders in the colony.

Monitoring scheme and biological inferences

We have illustrated the similarities and differences derived from different recapture methods in monitoring populations of a burrowing nesting seabird. In particular, how recapture processes influenced the level of heterogeneity among individuals and ultimately the estimate and precision of the demographic parameters. Overall, our results suggest that monitoring schemes should be designed in relation to the parameter and the precision desired. First, it would be important to assure continuity

over time. Gaps in capture-mark-recapture data can be easily accommodated in the capture-recapture models but they generate problems of parameter identifiability. This seems a trivial advice, but three out of the six long-term schemes analysed here had at least one gap in the capture-recapture time series (Appendix I), and this can be the case for many studies whose results have never been published. Also, the capture probability can be maximized by choosing the right period, site and number of visits to the colony. In some years and for some datasets, recapture probability was extremely low. As a rule of thumb, a capture probability less than 10% results in imprecise estimates of survival due to the covariation between these two parameters (Hargrove & Borland 1994). Estimates of resident survival can be obtained by repeated captures of individuals at their nest or in mist-nets, providing the structure of the capture-recapture model includes specific parameters for transient birds and, in specific cases, to accommodate recapture heterogeneity. Note that the use of mist nets, especially with the support of playback calls, results in a high number of captures, but it also increases the proportion of transient birds in the dataset. Consequently, estimates of survival of resident birds are usually less precise. Nevertheless, in the majority of storm petrel colonies nests are inaccessible to researchers and the use of mist-nets to monitor demographic parameters can be the only approximation available (Mitchell & Newton 2000). For the storm petrel, none of the capture methodology allowed to obtain informative estimates of population size. Their population trends can be more successful monitored by investigating the change in survival of resident birds (the most important predictor of population growth rate, see Saether & Bakke 2000), rather than by wide, weak estimates of population size (Tavecchia et al. 2008).

APPENDIX I:

Monitoring schemes of storm petrel in seven Mediterranean islands

Benidorm Island (colony B1 and B2) – The first two datasets come from Benidorm Island (Alicante, Spain, Fig. 1) where petrels concentrate in two natural caves, hereafter noted cave B1 and B2, respectively, about 150m apart. Most nest found inside both caves are accessible to researchers and a program began in 1993 with the aim of monitoring breeding birds in both caves (from 1994 in cave B2, see also Sanz-Aguilar et al. 2008, Sanz-Aguilar et al. 2009b). In 1996, a number of artificial nest-boxes were installed inside both caves to investigate if colony sizes were constraint by nest availability. The boxes were occupied mainly in cave B2 while it appears that the number of available nests is not a limiting factor in the larger colony (de León & Mínguez 2003). Also, there is some evidence that predation pressure by the Yellow legged gull *Larus michahellis* is higher in colony B1 (Mínguez 1994, Oro et al. 2005). In both colonies, breeding birds were caught annually at their nest principally during the incubation period. Although birds were caught only once, nests were monitored several times during incubation in order to catch both member of the pair and verify the breeding success (Table A1-1).

Marettimo Island (colony MA): At the colony at Marettimo Island (Egadi archipelago, Sicily, Italy, Fig. 1) marking and recapture of birds is conducted annually from 1991 to 2006, with the exception of 1995 (Lo Valvo & Massa 2000). The colony is visited once per year due to the difficult access (Table A1-1) and breeding adults are marked or recaptured during incubation or when attending recently hatched chicks. In 1997 a late visit to the colony resulted in only chicks ringed hence no recaptures of adults are available for that year. The colony is located inside a big cave where petrels nest in the ground and inside crevices.

Hormigas (colony HO) and Palomas (colony PA) Islands: At Hormigas (D) and Palomas(E) Islands (Murcia, Spain, Fig.1) petrels breed into generally inaccessible little caves and small crevices along the island and also on human structures on Hormigas. A regular mist-netting program began in 1996 on both islands. Capture

sessions were between April and August but the capture effort varied among years depending on sea conditions so that between-sessions intervals are, in some cases, larger than a year (Table A1-1). Number of nets varied between sessions but most common configurations were 3 mist-nets measuring 36-50 m at Palomas and 6-7 mist-nets measuring 84-100 m at Hormigas. Mist nets were usually placed on fixed points. Sampling was carried out between 1 hour before sunset and 1 hour after sunrise, so encompassing the whole activity period of storm petrels in the colony. Data records until 2004 were obtained form ANSE files and from 2005 onwards from Ringing Office.

Na Plana Island (colony NP): The last dataset came from the monitoring program at the island Na Plana (Cabrera Archipelago, Balearic Islands, Spain, Fig. 1). Here most of the storm petrels nest on island' coast in often unidentified or inaccessible caves and crevices (Amengual et al. 1999). From 1994 to 1998 an intensive mist-netting program was carried out during summer (June-September). Captures were carried out during dark moon nights and birds were lured into nets by petrel vocalisations played on a portable tape recorder installed between two nets of 20m in combined length from 10pm to 5am.

TABLE A1-1. Number of days of capture and storm petrels marked and recaptured per year at the study sites.

Colony - notation	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	Total
Number of days of capture																		
Benidorm (Alicante, Spain) - B1				20	38	13	14	7	9	10	16	4	20	4	8	14	19	196
Benidorm (Alicante, Spain) - B2					16	8	6	4	4	7	8	5	14	4	10	17	17	120
Marettimo (Sicily, Italy) - MA		1	1	1	2		1		1	1	1	1	1	1	1	1	1	13
Hormigas (Murcia, Spain) - HO							1	2		2	2				2	4	2	15
Palomas (Murcia, Spain) - PA							3	4	2	7	3				1	2	2	24
Na Plana (Cabrera, Spain) - NP					3	5	11	10	4									32
Number of birds captured																		
Benidorm (Alicante, Spain) - B1				169	224	136	124	113	127	109	99	78	67	49	63	139	173	1670
Benidorm (Alicante, Spain) - B2					52	30	20	9	12	31	19	53	51	58	78	115	144	672
Marettimo (Sicily, Italy) - MA		21	106	134	252		292		62	235	91	119	159	96	147	53	122	1889
Hormigas (Murcia, Spain) - HO							32	70		10	314				157	300	156	1039
Palomas (Murcia, Spain) - PA							65	212	28	139	437				125	174	317	1497
Na Plana (Cabrera, Spain) - NP					45	154	279	345	24									845
Proportion of already marked birds among the captures																		
Benidorm (Alicante, Spain) - B1				0	0.57	0.79	0.77	0.76	0.78	0.76	0.77	0.79	0.67	0.84	0.60	0.50	0.66	0.63
Benidorm (Alicante, Spain) - B2					0	0.47	0.70	0.67	0.75	0.45	0.74	0.30	0.67	0.69	0.60	0.60	0.68	0.56
Marettimo (Sicily, Italy) - MA		0	0	0.11	0.10		0.18		0.39	0.35	0.34	0.39	0.34	0.41	0.29	0.41	0.38	0.25
Hormigas (Murcia, Spain) - HO							0	0		0.40	0.23				0.18	0.44	0.61	0.32
Palomas (Murcia, Spain) - PA							0	0.04	0.14	0.09	0.10				0.11	0.19	0.26	0.13
Na Plana (Cabrera, Spain) - NP					0	0.01	0.10	0.20	0.46									0.13

APPENDIX II.

TABLE A2-1. Modelling local survival (noted ϕ' and ϕ for transient and resident birds respectively) and recapture probabilities (noted p) based on capture-recapture data from European storm petrels at the colonies of Benidorm (noted B1 and B2, respectively), Marettimo (MA), Hormigas (HO), Palomas (PA), and Na Plana (NP). Notation: np, number of parameters in the model; Dev = deviance; QAICc= Akaike's information criterion adjusted for small sample size (c) and overdispersion (Q); ΔQAICc=the difference in QAICc between the current and the model with the lowest QAICc; w_i=Akaike weigths,'t'=time effect, 'T'=linear trend in time, 'effort' = recapture effort (number of capture occasions per year). Symbol '+' indicates parallel variation, i.e. additive effect. Symbol '+' indicates interaction terms. The best model (highest QAICc weight) is shown in bold text.

Model-colony notation	recapture	survival	np	Dev	QAICc	ΔQAICc	w_i
1 -B1	p_t	$\phi'_t * \phi_t$	37	2723.19	1978.33	7.32	0.02
2 -B1	p	$\phi'_t * \phi_t$	26	2771.47	1990.09	19.08	0
3 -B1	p_{effort}	$\phi'_t * \phi_t$	27	2779.08	1997.41	26.40	0
4 -B1	p_t	$\phi'_t + \phi_t$	**27**	**2741.32**	**1971.01**	**0**	**0.93**
5 -B1	p_t	$\phi'_t * \phi$	27	2750.03	1977.1	6.09	0.04
6 -B1	p_t	$\phi' * \phi_t$	26	2772.08	1990.52	19.51	0
7 -B1	p_t	$\phi' * \phi$	15	2795.15	1984.65	13.64	0
1 -B2	p_t	$\phi'_t * \phi_t$	34	865.55	738.97	19.56	0
2 -B2	p_T	$\phi'_t * \phi_t$	25	874.88	728.21	8.8	0.01
3 -B2	p	$\phi'_t * \phi_t$	24	909.79	753.26	33.86	0
4 -B2	p_{effort}	$\phi'_t * \phi_t$	25	903.18	750.14	30.73	0
5 -B2	p_T	$\phi'_t + \phi_t$	**15**	**889.33**	**719.41**	**0**	**0.50**
6 -B2	p_T	$\phi'_t * \phi$	15	903.86	730.67	11.26	0
7 -B2	p_T	$\phi' * \phi_t$	14	892.05	719.52	0.11	0.48
8 -B2	p_T	$\phi' * \phi$	4	928.38	727.67	8.27	0.01
1 -MA	p_t	$\phi'_t * \phi_t$	36	3499.84	3342.88	0.21	0.47
2 -MA	p	$\phi'_t * \phi_t$	26	3554.6	3374.06	31.38	0
3 -MA	p_{effort}	$\phi'_t * \phi_t$	29	3643.39	3463.04	120.37	0
4 -MA	p_t	$\phi'_t + \phi_t$	29	3523.2	3350.71	8.03	0.01
5 -MA	p_t	$\phi'_t * \phi$	**27**	**3518.88**	**3342.67**	**0**	**0.52**
6 -MA	p_t	$\phi' * \phi_t$	28	3546.21	3370.22	27.55	0
7 -MA	p_t	$\phi' * \phi$	15	3590.31	3385.43	42.75	0
1 -HO	p_t	$\phi'_t * \phi_t$	15	1308.92	1338.92	1.94	0.27
2 -HO	p	$\phi'_t * \phi_t$	12	1506.11	1530.11	193.14	0
3 -HO	p_{effort}	$\phi'_t * \phi_t$	13	1453.66	1479.66	142.69	0
4 -HO	p_t	$\phi'_t + \phi_t$	13	1317.42	1343.42	6.44	0.03
5 -HO	p_t	$\phi'_t * \phi$	14	1326.63	1354.63	17.65	0
6 -HO	p_t	$\phi' * \phi_t$	**14**	**1308.98**	**1336.98**	**0**	**0.70**
7 -HO	p_t	$\phi' * \phi$	8	1359.72	1375.72	38.74	0

*Model-colony notation	recapture	survival	np	dev	QAICc	ΔQAICc	w_i
1 -PA	p_t	$\phi'_t * \phi_t$	19	1359.82	781.07	8.32	0.01
2 -PA	p	$\phi'_t * \phi_t$	14	1411.28	799.19	26.44	0
3 -PA	p_{effort}	$\phi'_t * \phi_t$	16	1409.93	802.45	29.7	0
4 -PA	p_t	$\phi'_t + \phi_t$	16	1364.99	777.9	5.14	0.06
5 -PA	p_t	$\phi'_t * \phi$	15	1366.82	776.9	4.14	0.10
6 -PA	p_t	$\phi' * \phi_t$	15	1374.81	781.26	8.51	0.01
7 -PA	**p_t**	**$\phi' * \phi$**	**9**	**1381.2**	**772.75**	**0**	**0.81**
1 -NP	p_t	$\phi'_t * \phi_t$	10	630.21	650.21	4.15	0.07
2 -NP	p	$\phi'_t * \phi_t$	8	645.32	661.32	15.26	0
3 -NP	p_{effort}	$\phi'_t * \phi_t$	9	634.77	652.77	6.71	0.02
4 -NP	p_t	$\phi'_t + \phi_t$	9	631.17	649.17	3.11	0.12
5 -NP	p_t	$\phi'_t * \phi$	9	630.94	648.94	2.88	0.13
6 -NP	p_t	$\phi' * \phi_t$	8	633.75	649.75	3.69	0.09
7 -NP	**p_t**	**$\phi' * \phi$**	**6**	**634.06**	**646.06**	**0.00**	**0.57**

Continue from page 51
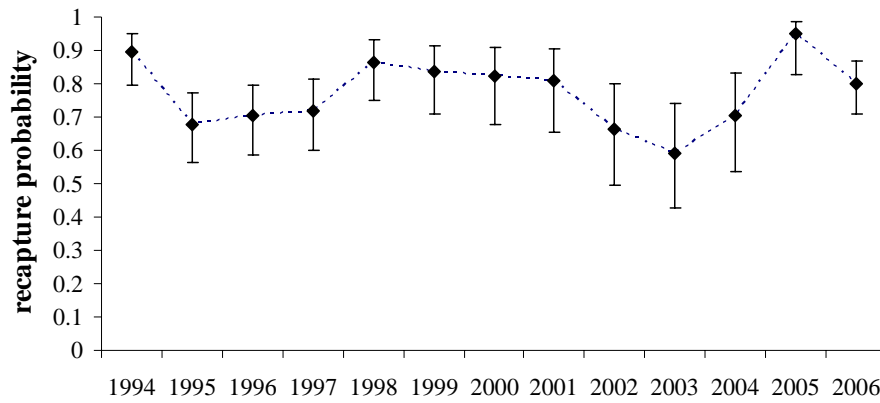
FIGURE A2-1a) Model averaged estimates of recapture probabilities during the study periods at colony B1(cave 1, Benidorm).
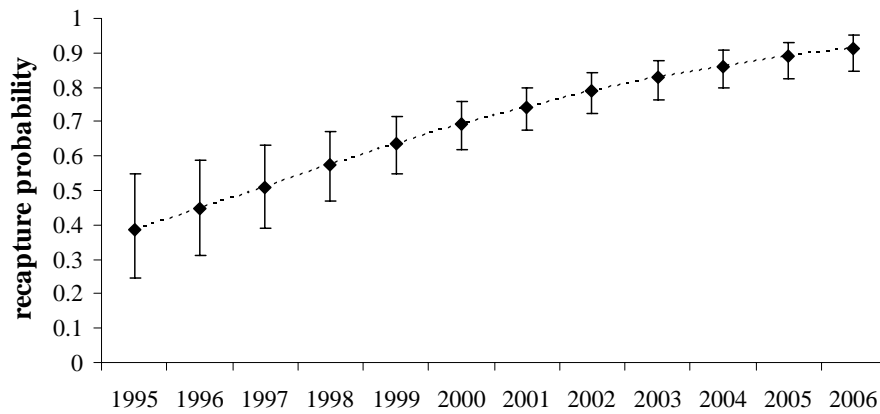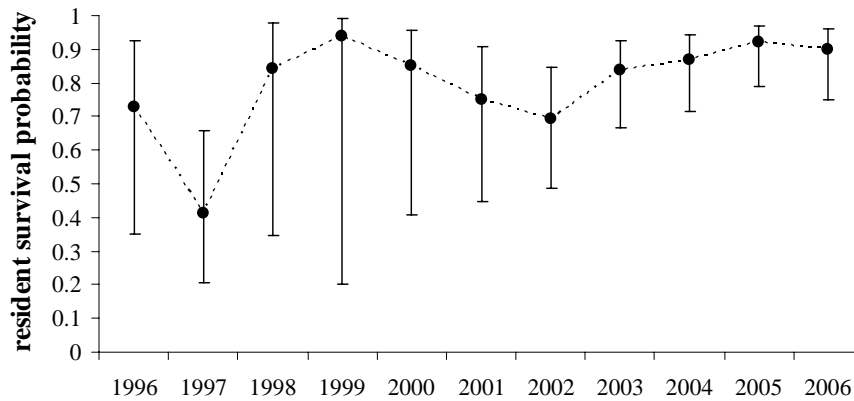

FIGURE A2-1b) Model averaged estimates of recapture probabilities during the study periods at colony B2 (cave 2, Benidorm).
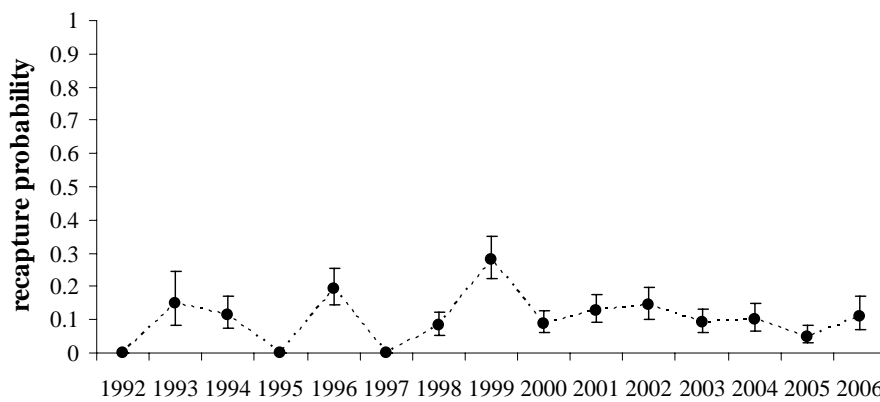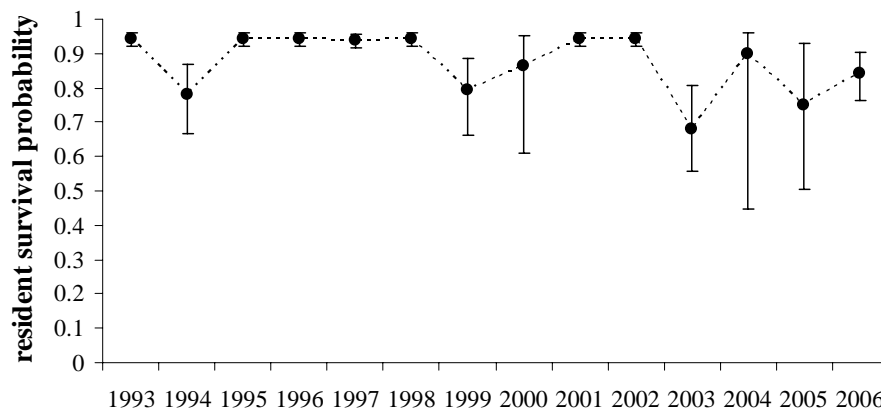

FIGURE A2-1c) Model averaged estimates of recapture probabilities during the study periods at colony MA (Marettimo).
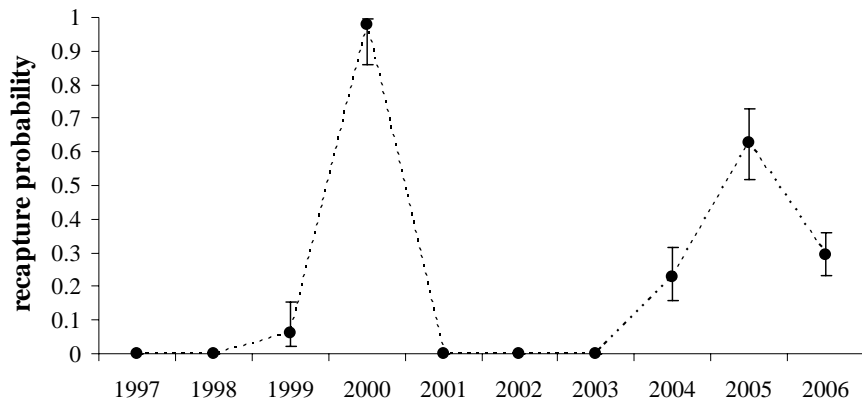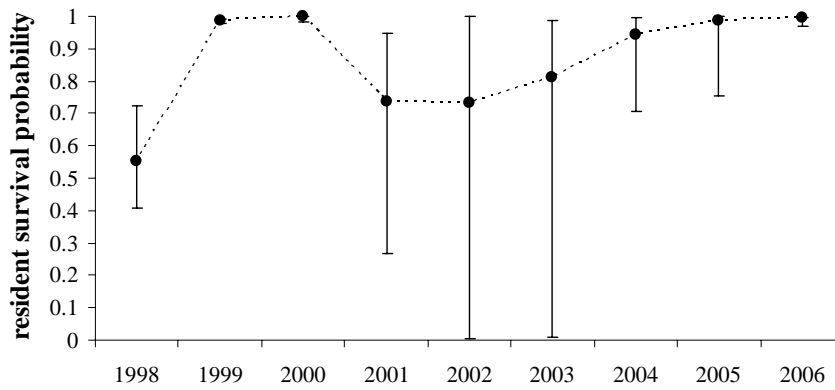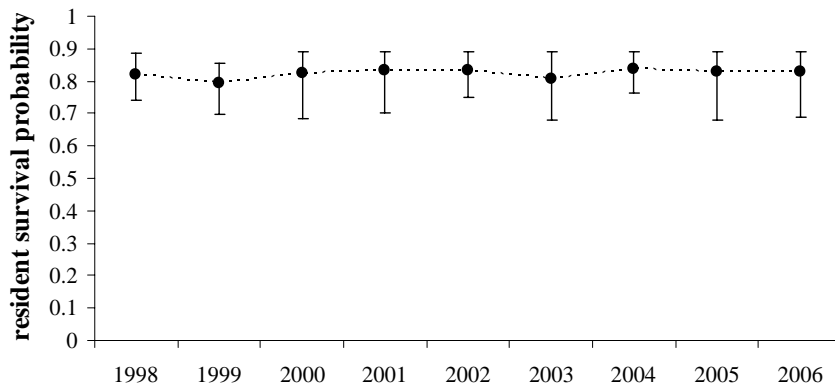
FIGURE A2-1d) Model averaged estimates of recapture probabilities during the study periods at colony HO (Hormigas).
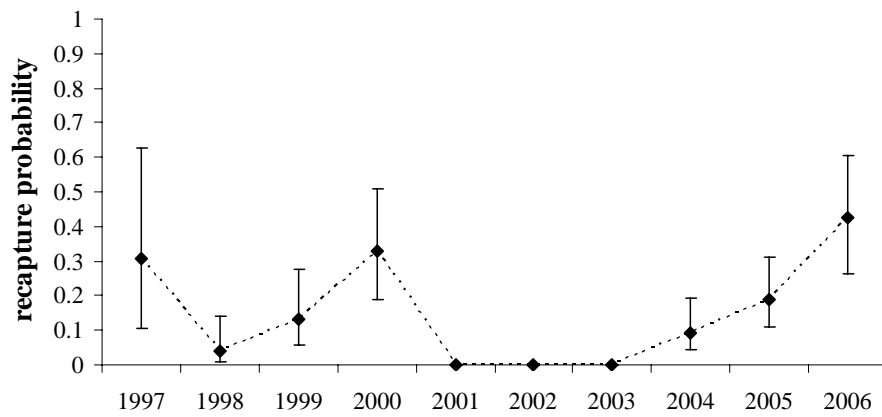
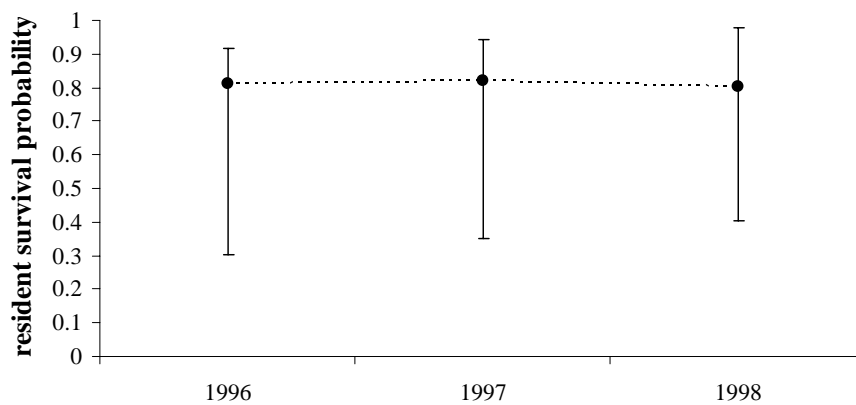**FIGURE A2-1e**) Model averaged estimates of recapture probabilities during the study periods at colony PA (Palomas).
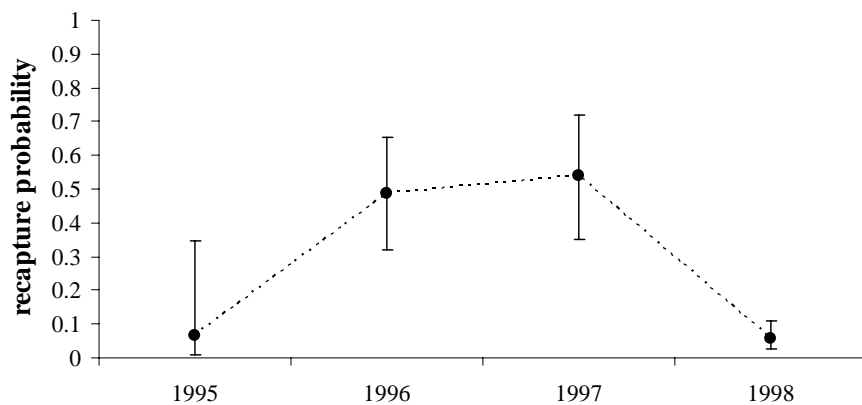
FIGURE A2-1f) Model averaged estimates of recapture probabilities during the study periods at colony NP (Na Plana).
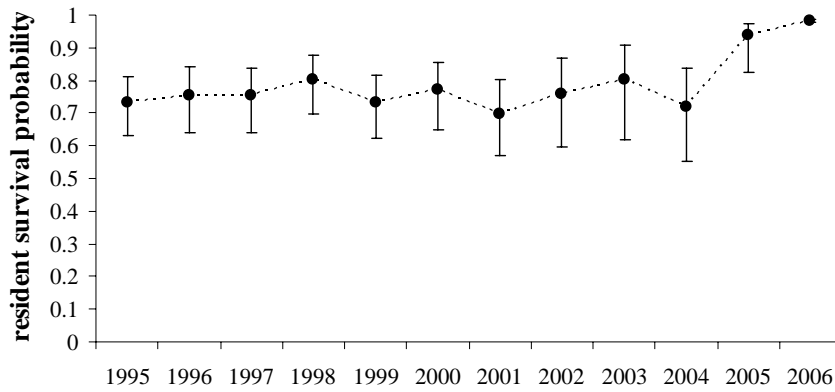
**FIGURE A2-2a)** Model averaged estimates of resident survival probabilities during the study periods at colony B1 (cave 1, Benidorm).

FIGURE A2-2b) Model averaged estimates of resident survival probabilities during the study periods at colony B2 (cave 2, Benidorm).

FIGURE A2-2c) Model averaged estimates of resident survival probabilities during the study periods at colony MA (Marettimo).

FIGURE A2-2d) Model averaged estimates of resident survival probabilities during the study periods at colony HO (Hormigas).

FIGURE A2-2e) Model averaged estimates of resident survival probabilities during the study periods at colony PA (Palomas).

FIGURE A2-2f) Model averaged estimates of resident survival probabilities during the study periods at colony NP (Na Plana).

Appendix III.
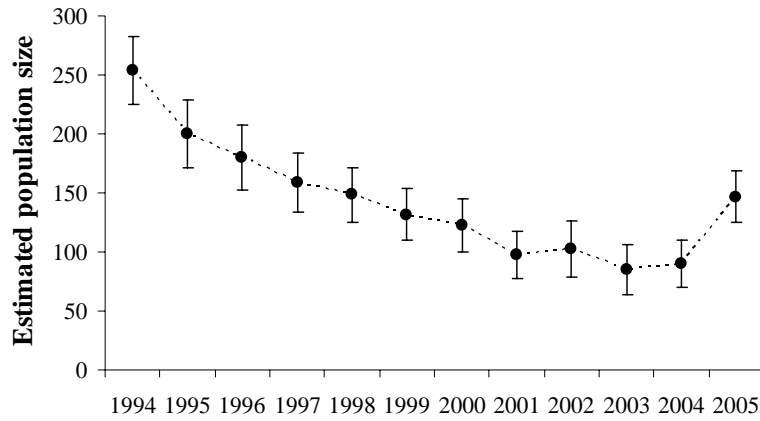
Figure A3-1a). Estimates of population size during the study periods at colony B1(cave 1, Benidorm).
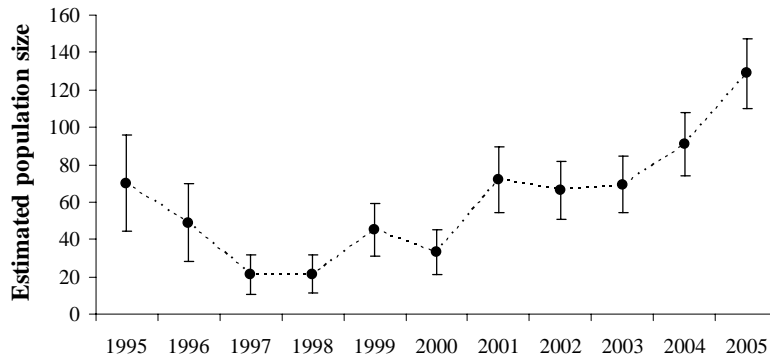
Figure A3-1b). Estimates of population size during the study periods at colony B2 (cave 2, Benidorm).
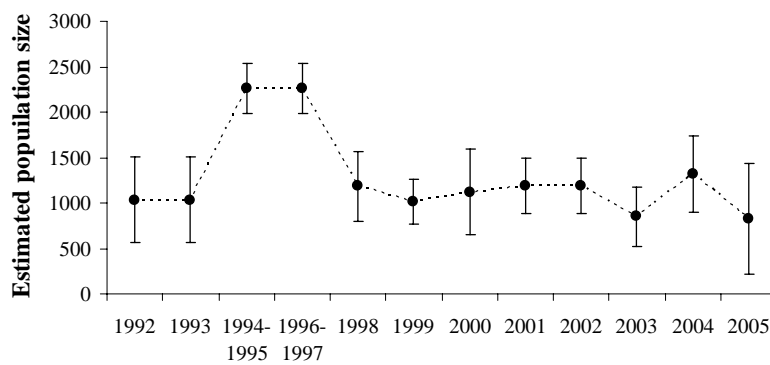
Figure A3-1c). Estimates of population size during the study periods at colony MA (Marettimo).
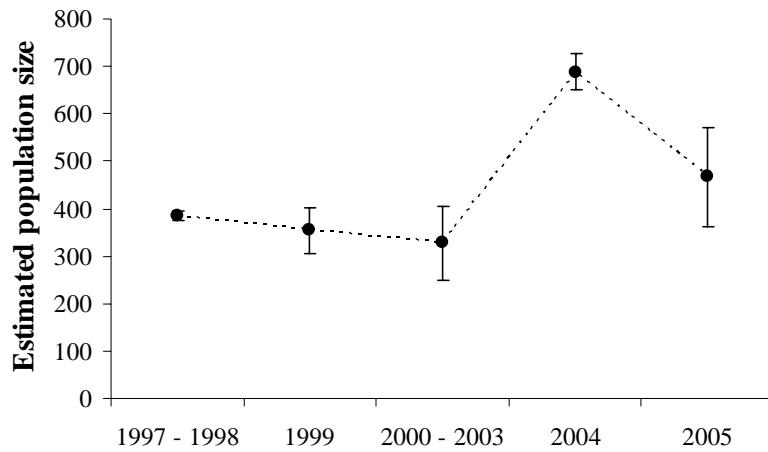
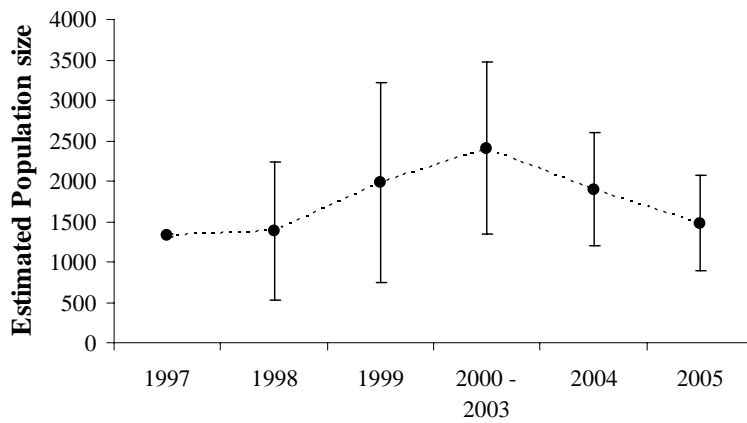**FIGURE A3-1d)**. Estimates of population size during the study periods at colony HO (Hormigas).

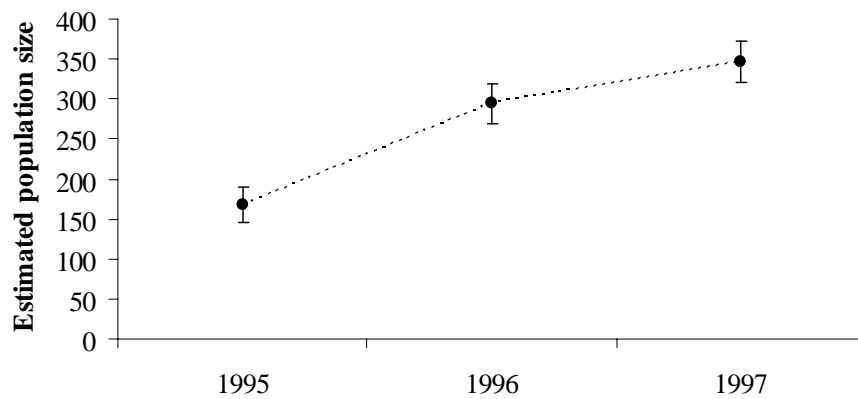**FIGURE A3-1e)**. Estimates of population size during the study periods at colony PA (Palomas).

FIGURE A3-1f). Estimates of population size during the study periods at colony NP (Na Plana).

CAPÍTULO 2

CONTRASTING AGE-SPECIFIC RECRUITMENT AND SURVIVAL AT DIFFERENT SPATIAL SCALES: A CASE STUDY WITH THE EUROPEAN STORM PETREL.

Contrasting age-specific recruitment and survival at different spatial scales: a case study with the European storm petrel.

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(**Ecography**, *in press)*

ABSTRACT

Evolutionary studies on optimal decisions or conservation guidelines are often derived by generalising patterns from a single population, while inter-population variability in life-history traits is seldom considered. We investigated here how survival and recruitment probabilities changed with age at different geographical scales using the encounter histories of 5523 European storm petrels from three Mediterranean colonies, and also how our estimates of these parameters might be expected to affect population growth rates using population matrix models. We recorded similar patterns among colonies, but also important biological differences. Local survival, recruitment and breeding success increased with age at all colonies; the most distant of three colonies (Marettimo Is.) showed the largest differences. Strikingly, differences in recruitment were also found between two adjacent colonies (two caves from Benidorm Is.). Birds marked as adults from Marettimo and Benidorm colonies had a different survival, whereas we found no differences within Benidorm. Differences in survival were no longer apparent between the two islands at the end of the study following a reduction in predation by specialist gulls at Benidorm. Since birds marked as fledglings mostly recruited near the end of the study, their overall survival was high and in turn similar among colonies. Results from our population matrix models suggested that different age-dependent patterns of demographic parameters can lead to similar population growth rates. Variability appeared to be greater for recruitment and the most sensitive parameter was adult survival. Thus conservation actions targeting this vulnerable species should focus on factors influencing adult survival. Differences in survival and recruitment among colonies could reflect the spatial heterogeneity in mortality due to predation and colony-specific density dependent processes. Results highlight the importance of taking into account the potential spatio-temporal heterogeneity among populations in vital rates, even in those traits that life-history theory considers less important in driving population dynamics.

Keywords: age of first reproduction, demographic parameters, inter-population variability, Mediterranean, population growth rate.

INTRODUCTION

In long-lived animals survival, accession to reproduction (recruitment) and breeding success are typically age-dependent (Newton 1989, Forslund & Pärt 1995). The age-dependent pattern determines the shape of the reproductive value function, i.e. the expected contribution to future generations from individuals of a given age, which ultimately drives optimal decisions on reproductive tactics (McNamara & Houston 1996). Moreover, the value and the shape of this function determine the expected population growth rate (Morris & Doak 2002). Consequently, age-related differences in demographic parameters should have important consequences for population persistence at a local as well as metapopulation level (Hanski & Gilpin 1997, Frederiksen et al. 2005, Tavecchia et al. 2005). In long-lived species the population growth rate is highly sensitive to changes in adult survival (Saether & Bakke 2000) but because natural selection tends to reduce the temporal variability in this parameter, population dynamics are driven mainly by changes in recruitment processes and/or fertility (Gaillard et al. 2000, Tavecchia et al. 2001, Weimerskirch 2002, Morris & Doak 2002, Oro et al. 2004a).

In addition to this life-history framework, constraints imposed by spatial variation in food resources, habitat availability or predator densities can generate differences in demographic rates at multiple geographical scales across populations of the same species (Levin 1981, Rodd & Reznick 1997, Ferrer et al. 2004, Tavecchia et al. 2008) or even within populations due for instance to despotic distributions (Oro 2008). An example of these phenomena is the large variation in survival, breeding success and population dynamics of nine populations of the black-legged kittiwake (*Rissa tridactyla*) across their geographical range (Frederiksen et al. 2005). Age of maturity, sex ratio, mortality rates and fecundity varied also among populations of guppies (*Poecilia reticulata*) according to predator pressure in each population (Reznick et al. 1990, Rodd & Reznick 1997), while the population structure in three groups of Soay sheep (*Ovis aries)* living in different parts of the same island was distinct, reflecting differences in survival, recruitment and dispersal rates (Coulson et al. 1999).

Results obtained from a single population can neither be taken as characteristic of the species nor exported to other populations without caution (Frederiksen et al. 2005, Breton et al. 2006). Further, comparative studies of inter-population variation in demographic parameters are necessary to improve our understanding of evolution of life histories, population functioning and finally the scale at which management actions can be effective, especially for those species whose abundance is notoriously difficult to monitor and where long-term trends remain generally undetected (Oro & Pradel 2000, Frederiksen & Bregnballe 2001, Cam et al. 2005, Frederiksen et al. 2005, Tavecchia et al. 2008).

The aim of this study was to assess the effects of age and site (colony) on probabilities of survival, recruitment and breeding success probabilities using data from the European storm petrel (*Hydrobates pelagicus*). We investigated the potential influence of spatial heterogeneity on demographic parameters by contrasting results from three colonies in the Mediterranean basin at two geographical scales: small (c. 0.15 km) and large (c. 1000 km). Estimates from these parameters were subsequently incorporated into an age-structured population model to evaluate if differences in demographic parameters among colonies may generate significant differences in the expected population growth rate.

METHODS

Data collection

The European storm petrel is one of the smallest long-lived seabirds of the Order Procellariiformes (average body mass, 28 g, Warham 1990). Storm petrels lay a single egg in natural borrows, under boulders or in crevices. The egg is incubated by both males and females for about 40 days (Warham 1990). There is no particular concern for the status of the species worldwide, but the Mediterranean subspecies, *H. p. melitensis*, is considered vulnerable due to its decline caused by predation from human introduced species (Martin et al. 2000). Here we used long-term individual data collected at three colonies in the Mediterranean basin (Fig. 1): one located on the island of Marettimo (Egadi archipelago, Italy, 37º58'N, 12º03'E); and two on the

island of Benidorm (southern Spain, 38° 30'N, 0° 08'E). The Marettimo colony is c. 1060 km east of Benidorm while the two colonies at Benidorm are c. 150 m apart. Individuals were captured on their nest during incubation or during the chick rearing period and marked with a stainless steel ring with a unique alpha-numeric code. Fledglings born in monitored nests were marked 20-50 days after hatching.
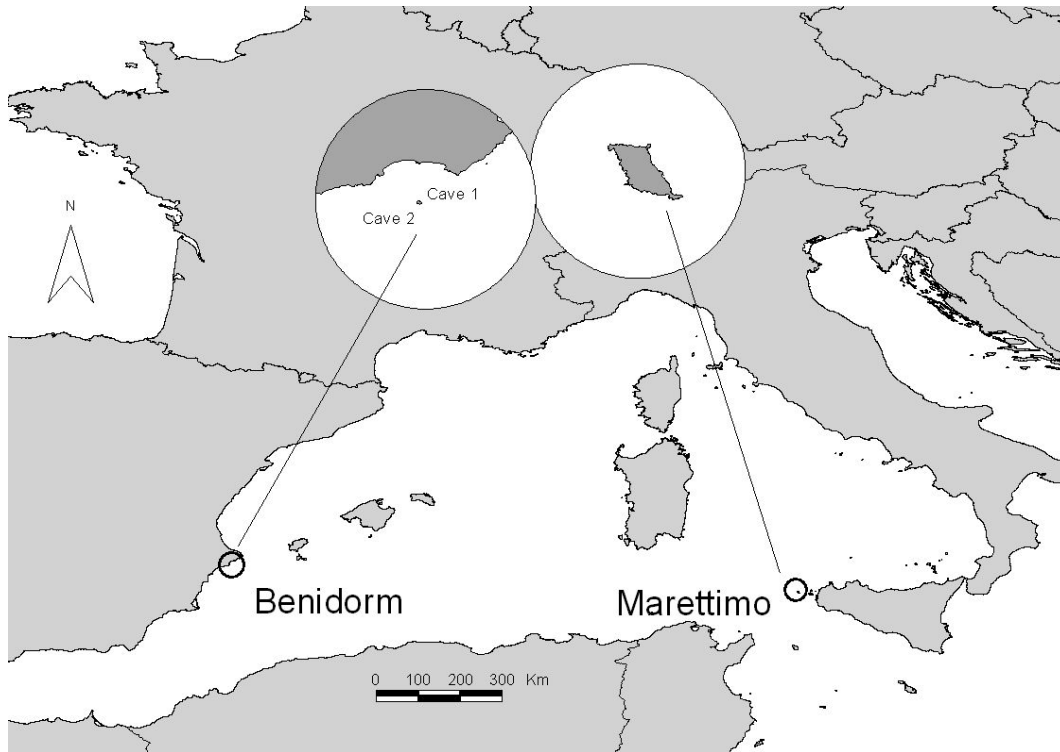

FIGURE 1. Location of the three study colonies: Marettimo Island (Italy) and Caves 1 and 2 in Benidorm Island (Spain).

Data collection at Marettimo Island.— Marking and recapture of birds at Marettimo Island was carried out from 1991-2006. Birds marked at Marettimo were divided into two groups, those ringed as fledglings (FM, for Fledgling Marettimo, n=2453) and those marked as adults (AM, for Adult Marettimo, n=1228). The colony was visited once per year except in 1994 when it was monitored twice and in 1995, when it was not visited. In 1997 the colony was visited late in the season when most of the adults had already left. These discrepancies are important as they influence what can be estimated from our data. Hence, for example, survival in 1994 and 1995-, are not separately estimable due to the absence of recaptures in 1995.

Data collection at Benidorm Island. — At Benidorm Island, data were collected during the period 1993-2006 at two breeding colonies, Cave 1 and Cave 2. The two colonies are not equivalent. Cave 1 hosts c. 200 breeding pairs, nearly twice the size of Cave 2, and is thought to have a higher predation pressure by the yellow legged gull *Larus michahellis* (Oro et al. 2005). Moreover, in 1996, a small number of artificial nest-boxes were installed inside both colonies but they were disproportionally occupied in Cave 2 (de León & Mínguez 2003). As in Marettimo, birds marked at Benidorm from 1993-2006 were divided into two groups, those ringed as fledglings in Cave 1 (FB1, for Fledgling of Benidorm at Cave 1, n=649) and in Cave 2 (FB2, n=332); and those, of unknown age, marked as adults in both colonies (AB1, n=593 and AB2, n=268, for Adult of Benidorm in Cave 1 and 2, respectively). With the exception of one case (discarded in the present analysis), adults caught in one colony were never observed in the other. We recorded only three cases of natal dispersal, fledglings marked in one Cave and found breeding in the other. These birds were assigned to the colony where they recruited. Due to difficulties associated with accessing Marettimo, breeding outcomes were only recorded at Benidorm Island and these were acquired by inspecting nests during the hatching and fledging breeding periods. Nests in which the egg did not hatch or in which individuals failed to rear their chick were considered unsuccessful (see details in Sanz-Aguilar et al. 2008). Finally, thirty-seven breeding adults and ninety-two fledglings were sexed by DNA technique (see details in Griffiths et al. 1998).

<u>*Statistical analysis*</u>

Capture-mark-recapture analysis

   Local survival (survival confounded by permanent immigration out of the study areas) and recapture probabilities from birds marked at the three study sites were assessed by capture-mark-recapture analyses (e.g. Lebreton et al. 1992, Amstrup et al. 2005). We performed two separate analyses, one for birds marked as fledglings and a second for birds marked as adults. Although capture-mark-recapture models can be used to analyze recruitment and population growth rate (Hilton & Miller 2003), the small sample size on birds marked as fledglings precluded such analysis, and recruitment was analyzed separately (see below).

Goodness-of-fit. — Capture-recapture analyses typically begin with a goodness-of-fit of a model assuming full time variation for all parameters (the Cormark-Jolly-Seber (CJS) model, Lebreton et al. 1992). The goodness-of-fit test is based on specific contingency tables for each recapture occasion which can be calculated using program U-CARE 2.2.2 (Choquet et al. 2005). The program includes a specific test for transience (Test 3.SR) which assesses whether survival soon after marking is different from survival thereafter, and for trap-dependence (Test 2.CT) which tests whether recapture probability at time i depends on the past capture history (see more details in Appendix I). With the exception of group AB2, we found a significant transient effect in all groups (Appendix I). In birds marked as fledglings, a transient effect represents a lower local survival of youngest birds while in birds marked as breeders transience may reflect colony abandonment (birds leaving the study area), low survival in response to the capture, and/or a survival cost of first reproduction (Pradel et al. 1997, Sanz-Aguilar et al. 2008). To appropriately account for transience in our data, we modified our starting CJS model to include an effect of age for all groups except AB2. Remaining heterogeneity was accounted for by scaling model deviances using a variance inflation factor, $\hat{c}$: $\hat{c}$ =1.45 for birds marked as fledglings and $\hat{c}$ =1.26 for birds marked as adults (Appendix I).

Model selection procedure. — Model selection was based on the Akaike's Information Criterion adjusted for small sample size (c) and overdispersion (Q) calculated as:

$$QAIC_c = \frac{dev}{\hat{c}} + 2 * np$$

where *dev* is model deviance; $\hat{c}$ is the variance inflation factor; and *np* the number of separately identifiable parameters in the model (Burnham & Anderson 2002). Models were built and fit to the data using program M-SURGE (Choquet et al. 2004, Choquet et al. 2006). Additionally for each model i, we calculated the Akaike weights, w_i, as an index of its relative plausibility (Burnham & Anderson 2002). Estimates of survival and recapture probabilities were obtained by model averaging in which each model contributed to the final estimate according to its Akaike weight (Burnham &

Anderson 2002). Evidence ratios were calculated to measure the magnitude of the difference between model-i and model-j as w_i/w_j.

Analysis of birds marked as fledglings. —Despite the high number of petrels marked as fledglings (n=3434), less than 8% were later recaptured as breeders (7% and 6% at Marettimo and Benidorm, respectively). For this reason we built models without the effect of time on survival and recapture parameters, with the exception of the model to assess the goodness-of-fit. Recapture probability in 1995 and 1997 at Marettimo was fixed to '0'. In addition, we set survival of ages 1 and 2 from birds at Marettimo equal given the low number of birds that recruited before age 3. At Benidorm recapture parameters for age 1 and 2 were fixed to 0 since no birds were caught recruiting before 3 years old; consequently only the product of survival from age 1-3 was estimable from our analysis of the Benidorm fledgling dataset. Survival of birds aged from 3 to 15 at Marettimo and from 4 to 13 in Caves 1 and 2 at Benidorm were combined in a single age class for each colony. We began by modelling the effect of age on recapture probability and then we modelled the effect of the colony on survival. For recapture probability we considered up to 6 age classes (from 1 to 5 years old, older birds grouped together); additional classes did not improve model fit (results not shown). As we had not *a priori* biological information or hypotheses about the age-dependent patterns of recruitment (i.e. the age-dependent capture probability) and several models with different recapture structures were tied in terms of QAICc (see Results), we tested models including all the structures of recapture and survival tied; finally we calculated averaged parameter estimates of such models.

Analysis of birds marked as adults. —The analysis of birds marked as adults followed the same procedure of the one of birds marked as fledgling. The high number of petrels marked as adults, and their high recapture probabilities allowed an extensive modelling of the effects considered without additional assumptions.

Recruitment probabilities

The observed number of birds that recruited at different ages to their natal colonies (Fig. 2a) cannot be taken as an estimate of the age-dependent recruitment because a certain number of birds may breed undetected. Clobert et al. (1994)

proposed a method that makes use of the age-dependent capture probability, p_j, to estimate the recruitment probabilities, B_j, at age j. Assuming that full recruitment is attained at age k and birds of this age do not skip reproduction, B_j can be estimated as the ratio p_j/p_k. Variance of B_j can be calculated using the δ-method (Morgan 2000). Although the method is not reliable for long-lived species that breed intermittently (Clobert et al. 1994), recent evidence indicated that reproductive skipping in the European storm petrel is rare (Sanz-Aguilar et al. 2008).
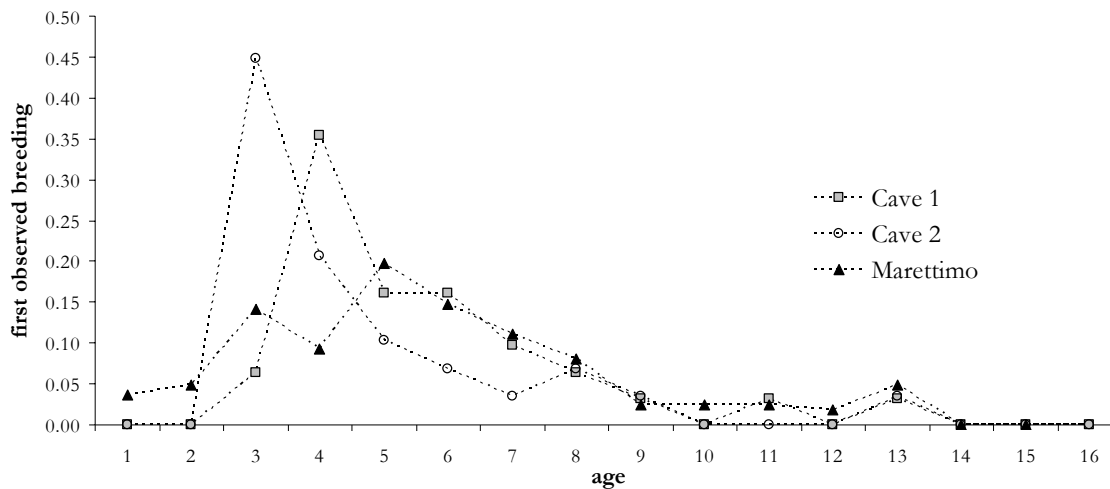

FIGURE 2a. Age-dependent proportion of first observed breeding at Marettimo and at Caves 1 and 2 at Benidorm Island. About 7% and 6% of the birds marked at fledging returned to breed at their natal colony in Marettimo (n=169) and Benidorm Island (n=60), respectively.

Breeding success and sex ratio at fledgling

We applied generalized linear mixed models (McCulloch & Searle 2001) to examine the effect of breeding colony and age on breeding success using data from 60 breeding adults marked as fledglings collected at Benidorm. Breeding success was modelled as a binary variable (1=successful, 0=unsuccessful) using a logit-link function with binomial error distribution and the glmmML function available in the open source software R (www.R-project.org/). Individual identity was treated as a random effect to correct for the multiple entries from the same birds and age (5 classes, for birds aged 3, 4, 5, 6, and older) and breeding colony as fixed effects. Model selection followed the same procedure and criteria as in capture-mark-recapture analyses (see above). In addition, using data from 92 molecularly sexed

fledglings born in 2005 at Benidorm, sex ratio was obtained as the mean and 95% credible intervals of the posterior distribution of the parameter (i.e. female proportion) calculated by means of Markov Chain Monte Carlo simulations using the Bayesian software WinBUGS 14, after running 100,000 iterations. Since we had no prior information on the study system regarding sex ratio we modelled the marginal distribution of the parameter by means of a uniform distribution [0, 1].

Population matrix modelling

We combined model averaged estimates of survival, recruitment and breeding success from the analyses of birds ringed as fledglings into a demographic matrix model to calculate a colony specific growth rates, λ (Caswell 2001). The variance of λ was estimated as $\Sigma\left(\dfrac{\partial\lambda}{\partial\theta}\right)^2 \sigma_\theta^2$, where σ_θ^2 was the variance of the element of the matrix and $\dfrac{\partial\lambda}{\partial\theta}$, its sensitivity, i.e. the effect of a change in a given parameter of the model on λ (Lande 1988b). Note that the breeding success of birds breeding at Marettimo was not available so we used instead the low predation pressure value from Benidorm (Cave 2; see Table A2 in Appendix II).

RESULTS

Capture-mark-recapture analysis

Analysis of birds marked as fledglings. —Observed natal philopatry, i.e. the proportion of birds marked as young that came back to their natal colony to breed and were detected, was similar between Marettimo and Benidorm, 7% and 6% respectively. Most of the birds marked as fledglings that came back to breed at their natal colonies, did so toward the end of the study: at Marettimo the median of the distribution of returns from 1993 to 2006 was 2002; at Cave 1 and Cave 2 at Benidorm medians were 2002 and 2005 respectively. Despite the proximity of the two cave colonies at Benidorm, observed natal philopatry at Benidorm was high: about 95% of the captured birds that returned (96.7% and 93.3% in Cave 1 and Cave 2, respectively) recruited into their natal colony. Extremely high natal philopatry was

also observed at Marettimo, where most birds recruited in the same area of the cave where they hatched (Lo Valvo & Massa 2000). Data from Benidorm suggested that males are more philopatric than females (67% of birds recaptured as breeders were males, $\chi_1^2 = 4.568$, P=0.03). Part of this difference may be due to the fact that the sex ratio at fledgling was male biased. Indeed, when the proportion of philopatric birds was related to sex ratio at fledging (see below) we did not find significant differences in philopatry between sexes ($\chi_1^2 = 2.099$, P=0.15). There was a marked difference in the earliest observed age of first breeding between the three colonies (Fig 2a): the earliest detected age of first reproduction at Benidorm Island was 3 while in Marettimo 2.7 ‰ (6/2264) of the petrels came back to breed at age 1.

We began the capture-recapture analyses by modelling recapture probabilities at Marettimo (models 1F to 6F; Table 1). Including the effect of age in recapture probability reduced substantially the QAICc values (models 2F to 6F; Table 1). A model in which recapture parameters varied as a function of age until age 5 (model 5F; Table 1) presented the lowest QAICc. From such model we selected the structure of recapture probabilities for Marettimo to modelling recapture probabilities at both Benidorm colonies, although model 5F was tied in terms of QAICc with models 3F, 4F and 6F (Table 1). For the data from Cave 1, the model that presented the lowest QAICc was model 7F (Table 1), in which recapture parameters varied as a function of age until age 4. This model was selected to modelling recapture probabilities at Cave 2, although the model was tied with models 8F and 9F (Table 1) in terms of QAICc. Model 7F (3 age classes) was also the best model in terms of QAICc for the data from Cave 2 (Table 1) but again other models (models 10F, 11F and 12F, Table 1) were supported.

Model	recapture	survival	np	Dev	QAICc	ΔQAICc	w_i
1F	M / B1 / B2	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	9	2919.85	2031.7	68.00	0.00
2F	M a(1,2:15) / B1 / B2	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	10	2867.39	1997.5	33.82	0.00
3F	M a(1_2,3:15) / B1 / B2	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	11	2838.28	1979.4	15.74	0.00
4F	M a(1_3,4:15) / B1 / B2	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	12	2835.82	1979.7	16.05	0.00
5F	M a(1_4,5:15) / B1 / B2	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	13	2828.69	1976.8	13.13	0.00
6F	M a(1_5,6:15) / B1 / B2	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	14	2828.69	1978.8	15.13	0.00
7F	M a(1_4,5:15) / B1 a(3, 4:13) / B2	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	14	2807.31	1964.1	0.39	0.11
8F	M a(1_4, 5:15) / B1 a(3_4, 5:13) / B2	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	15	2805.65	1964.9	1.24	0.07
9F	M a(1_4,5:15) / B1 a(3_5, 6:13) / B2	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	16	2805.6	1966.9	3.21	0.03
10F	M a(1_4,5:15) / B1 a(3,4:13) / B2 a(3,4:13)	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	15	2807.25	1966	2.34	0.04
11F	M a(1_4,5:15) / B1 a(3,4:13) / B2 a(3_4,5:13)	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	16	2807.24	1968	4.34	0.02
12F	M a(1_4,5:15) / B1 a(3,4:13) / B2 a(3_5,6:13)	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	17	2807.01	1969.9	6.18	0.01
13F	M a(1_4,5:15) / B1 a(3,4:13) / B2	M a(1:2,3:15) / B1 a(1:3,4:13) = B2 a(1:3,4:13)	12	2820.03	1968.9	5.16	0.01
14F	**M a(1_4,5:15) / B1 a(3,4:13) / B2**	**M a(1:2,3:15) = B2 a(1:3,4:13) /B1 a(1:3,4:13)**	**12**	**2812.55**	**1963.7**	**0.00**	**0.14**
15F	M a(1_4,5:15) / B1 a(3,4:13) / B2	M a(1:2,3:15) = B1 a(1:3,4:13) = B2 a(1:3,4:13)	10	2825.25	1968.5	4.76	0.01
16F	M a(1_2,3:15) / B1(3, 4:13) / B2	M a(1:2,3:15) = B2 a(1:3,4:13) /B1 a(1:3,4:13)	10	2819.19	1964.26	0.57	0.10
17F	M a(1_3,4:15) / B1(3, 4:13) / B2	M a(1:2,3:15) = B2 a(1:3,4:13) /B1 a(1:3,4:13)	11	2817.58	1965.26	1.57	0.06
18F	M a(1_5,6:15) / B1 a(3,4:13) / B2	M a(1:2,3:15) = B2 a(1:3,4:13) /B1 a(1:3,4:13)	13	2812.09	1965.37	1.68	0.06
19F	M a(1_4, 5:15) / B1 a(3_4, 5:13) / B2	M a(1:2,3:15) = B2 a(1:3,4:13) /B1 a(1:3,4:13)	13	2810.89	1964.55	0.86	0.09
20F	M a(1_4,5:15) / B1 a(3_5, 6:13) / B2	M a(1:2,3:15) = B2 a(1:3,4:13) /B1 a(1:3,4:13)	14	2810.84	1966.51	2.82	0.03
21F	M a(1_4,5:15) / B1 a(3,4:13) / B2 a(3,4:13)	M a(1:2,3:15) = B2 a(1:3,4:13) /B1 a(1:3,4:13)	13	2811.73	1965.12	1.43	0.07
22F	M a(1_4,5:15) / B1 a(3,4:13) / B2 a(3_4,5:13)	M a(1:2,3:15) = B2 a(1:3,4:13) /B1 a(1:3,4:13)	14	2811.56	1967.01	3.32	0.03
23F	M a(1_4,5:15) / B1 a(3,4:13) / B2 a(3_5,6:13)	M a(1:2,3:15) = B2 a(1:3,4:13) /B1 a(1:3,4:13)	15	2811.55	1969.00	5.31	0.01
24F	M a(1_2,3:15) / B1(3, 4:13) / B2	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	12	2816.90	1966.69	3.00	0.03
25F	M a(1_3,4:15) / B1(3, 4:13) / B2	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	13	2814.44	1967.00	3.30	0.03
26F	M a(1_5,6:15) / B1 a(3,4:13) / B2	M a(1:2,3:15) / B1 a(1:3,4:13) / B2 a(1:3,4:13)	15	2807.30	1966.07	2.38	0.04

TABLE 1. Modelling local survival and recapture probabilities based on capture-recapture data from birds marked as fledglings at three colonies (Caves 1 and 2 at Benidorm Island, Spain, noted B1 and B2, and one colony at Marettimo, Italy, denoted M). Notation: np, number of parameters in the model; Dev = deviance; QAICc= Akaike's information criterion adjusted for small sample size (c) and overdispersion (Q); ΔQAICc=the difference in QAICc between the current and the model with the lowest QAICc; w_i=Akaike weigths, 't'=time effect, 'a' = age effect. Age structure is summarized in parentheses: the notation i:j means that the structure assumed a single parameter from age i to age j , while the notation i_j indicates that there is a parameter from each age class from i to j. For example, the notation 'a(1:2,3_15)' indicates two specific parameters, one for birds aged 1 and 2 years old and a second for birds older than 2. Note that recapture probability of birds aged 1 and 2 was fixed to 0 at Benidorm colonies as no birds came back to breed before age 3. Colony specific parameters are separated by the symbol '/'. Symbol '/+/' indicates parallel variation among colonies and models without this notation include colony interaction terms. Symbol '=' indicates equality among groups (i.e. colonies). The best model (highest QAICc weight) is shown in bold text.

For survival, Akaike weights marginally supported a model in which survival differed across colonies at Benidorm Island but Cave 2 was similar to the estimate from Marettimo (model 14F; Table 1). Overall, models 7F, 13F, and 15F were also supported. At this point, in order to take into account uncertainty in model selection, we built new models including different combinations of the structures of recapture and survival probabilities that were previously supported (models 16F to 27F; Table 1). Note that models with other possible combinations of recapture and survival structures were not retained (Akaike weights lower than 0.1, results not shown). Model 14F (Table 1) was the best in terms of QAICc *w*, nevertheless models 7F to 13F and 15F to 26F (Table 1) were also supported, so we calculated model averaged estimates of recapture and survival probabilities from the full model set. Model averaged estimates of survival probabilities indicated a survival probability of 0.57 (SE: 0.05) for birds aged 1 and 0.89 (SE: 0.03) from birds older than 2 years old in Marettimo; 0.47 (SE: 0.04) and 0.55 (SE: 0.03) for birds aged less than 4 and 0.86 (SE: 0.04) and 0.94 (SE: 0.01) for older birds breeding in Caves 1 and 2, respectively.
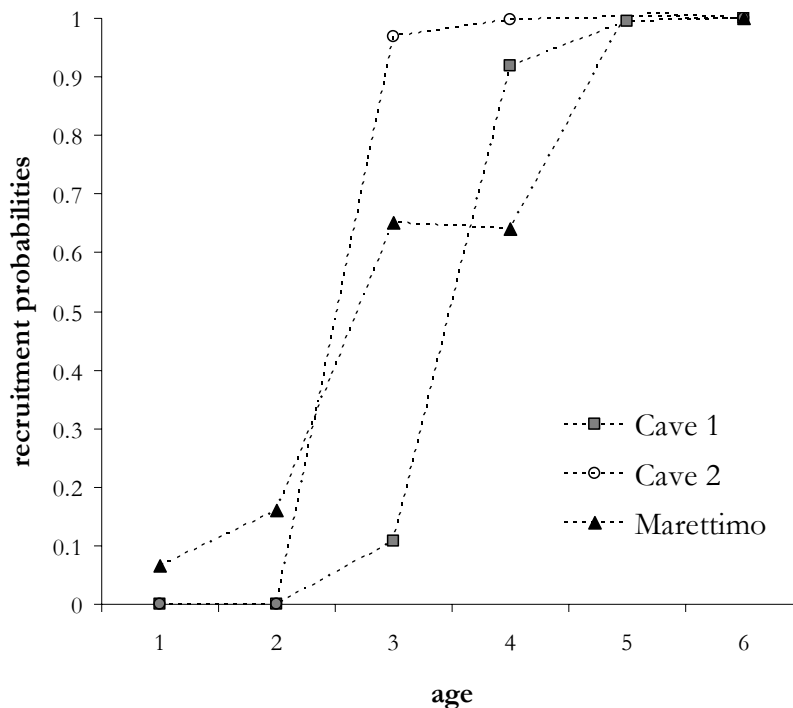

FIGURE 2b. Age-dependent recruitment probabilities of European storm petrels breeding at Marettimo and at Cave 1 and Cave 2 at Benidorm Island.

The observed number of petrels that returned to the colonies (i.e. without correcting for recapture probabilities) is shown in Fig 2a. This pattern was in agreement to the model averaged estimates of recapture probability, which we used to estimate recruitment probabilities: although petrels in Benidorm Island started to breed at older ages than in Marettimo, the analysis indicated that the full recruitment was reached earlier (Fig 2b; Table A2 Appendix II).

Analysis of birds marked as adults. —We started the analysis by modelling recapture probabilities (model 1A, Table 2). Following previous analysis of these data (Tavecchia et al. 2008) we used a linear trend to model recapture probabilities from Cave 2 (Benidorm); annual variation was fitted to Marettimo and in Cave 1 (model 2A; Table 2). Models without time effects in recapture probabilities were strongly rejected (ΔQAICc higher than 10, results not shown). It is likely that the linear increase of the recapture probabilities in Cave 2 was due to the progressive occupancy of artificial nest boxes that did not occur in Cave 1 (Tavecchia et al. 2008, Fig 3a). At Marettimo and in Cave 1 from Benidorm recapture probabilities varied annually, probably due to differences in field effort invested in capture (Fig 3a).
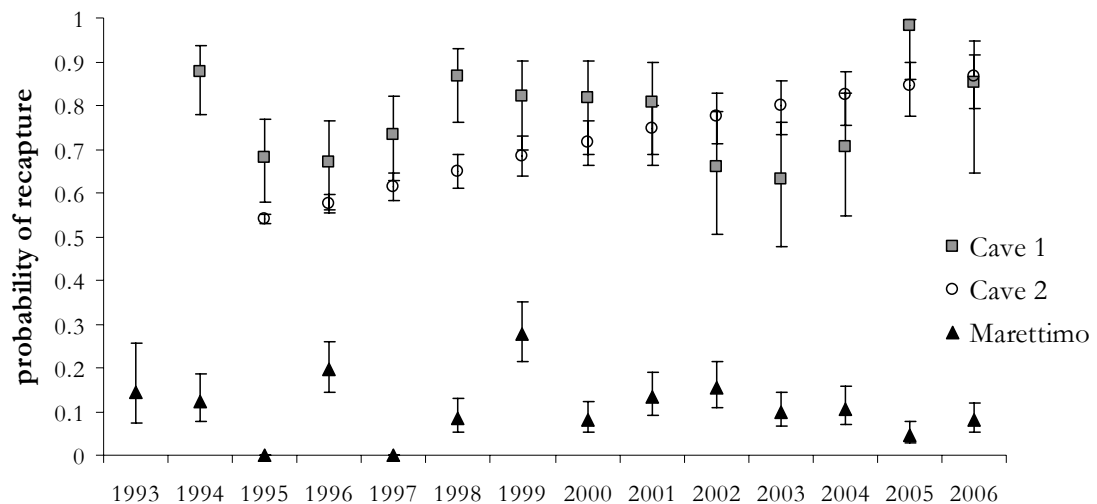

FIGURE 3a. Model averaged estimates on recapture probabilities of European storm petrels marked as adults, breeding at Marettimo, Italy, and Caves 1 and 2 at Benidorm Island, Spain. Model averaged estimates were obtained through capture-recapture modelling (Table 2).
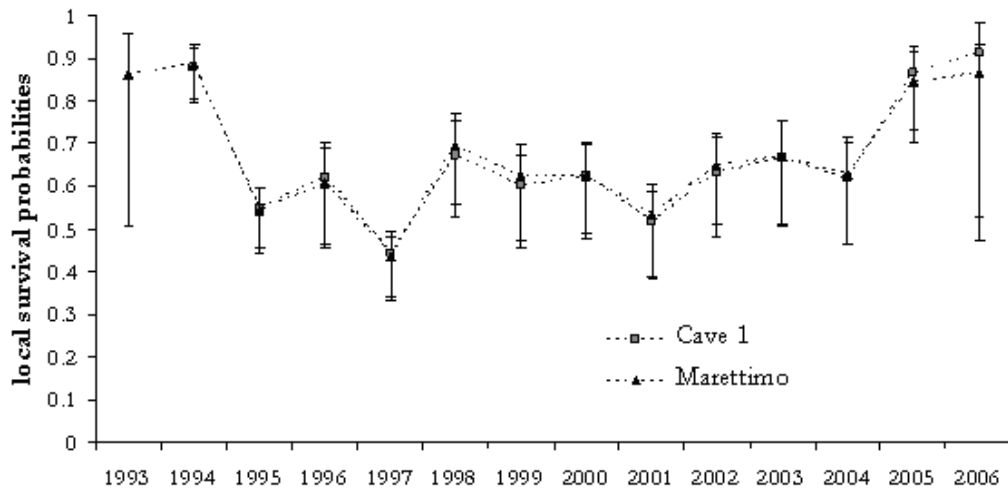
FIGURE 3b. Model averaged estimates on local survival probabilities of newly marked European storm petrels individuals (marked as adults), breeding at Marettimo, Italy, and Caves 1 at Benidorm Island, Spain. Model averaged estimates were obtained through capture-recapture modelling (Table 2).
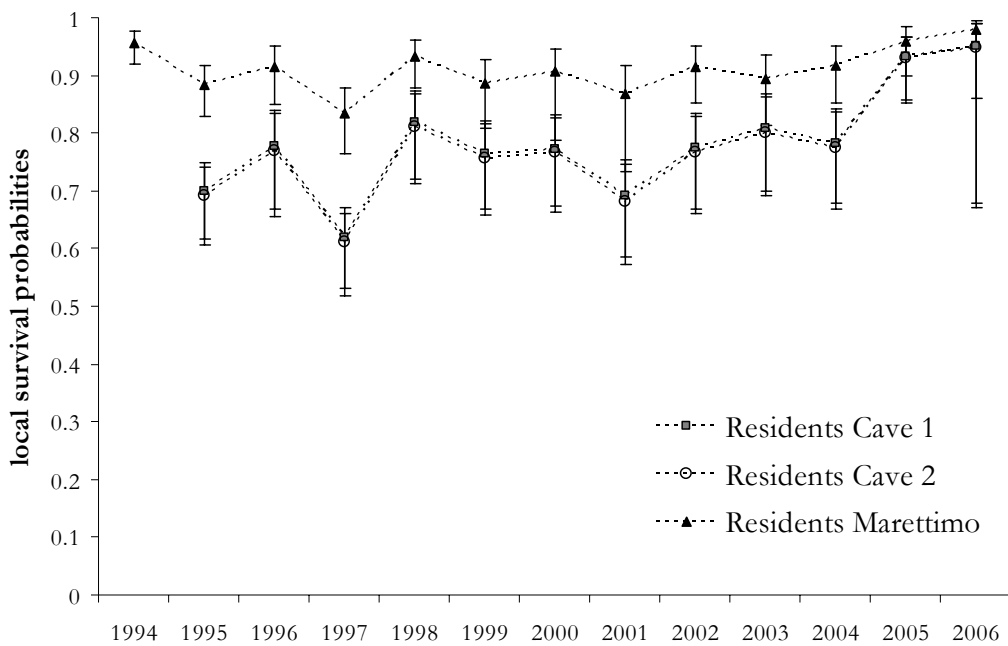

FIGURE 3c. Model averaged estimates on local survival probabilities of resident European storm petrels (marked as adults), breeding at Marettimo, Italy, and Caves 1 and 2 at Benidorm Island, Spain. Model averaged estimates were obtained through capture-recapture modelling (Table 2).

TABLE 2. Modelling local survival and recapture probabilities based on capture-recapture data from birds marked as adults at three colonies (Caves 1 and 2 at Benidorm Island, Spain, noted B1 and B2, and one colony at Marettimo, Italy, denoted M. Notation: np, number of parameters in the model; Dev = deviance; QAICc= Akaike's information criterion adjusted for small sample size (c) and overdispersion (Q); ΔQAICc=the difference in QAICc between the current and the model with the lowest QAICc; w_i=Akaike weigths, 't'=time effect. In addition superscript 'tr' and 'res' indicate parameters for transients and resident respectively. A linear trend in time was noted 'T'. 'Colony specific parameters are separated by the symbol '/'. Symbol '/+/' indicates parallel variation among colonies and models without this notation include colony interaction terms. Symbol '=' indicates equality among groups (i.e. colonies). Model with the highest w is in bold.

Model	recapture	survival	np	Dev	QAICc	ΔQAICc	w_i
1A	M (t) / B1 (t)/ B2 (T)	M_{tr} (t) / $B1_{tr}$ (t) / M_{res} (t) / $B1_{res}$ (t) / $B2_{res}$ (t)	94	6645.07	5461.86	22.62	0.00
2A	M (t) / B1 (t)/ B2 (T)	M_{tr} (t) / $B1_{tr}$ (t) / M_{res} (t) / $B1_{res}$ (t) / $B2_{res}$ (t)	84	6658.36	5452.41	13.16	0.00
3A	M (t) / B1 (t)/ B2 (T)	M_{tr} (t) = $B1_{tr}$ (t) / M_{res} (t) / $B1_{res}$ (t) / $B2_{res}$ (t)	76	6680.55	5454.02	14.77	0.00
4A	M (t) / B1 (t)/ B2 (T)	M_{tr} (t) / $B1_{tr}$ (t) / M_{res} (t) = $B1_{res}$ (t) = $B2_{res}$ (t)	64	6751.21	5486.10	46.85	0.00
5A	M (t) / B1 (t)/ B2 (T)	M_{tr} (t) / $B1_{tr}$ (t) / M_{res} (t) / $B1_{res}$ (t) = $B2_{res}$ (t)	73	6675.87	5444.31	5.06	0.05
6A	M (t) / B1 (t)/ B2 (T)	M_{tr} (t) = $B1_{tr}$ (t) / M_{res} (t) / $B1_{res}$ (t) = $B2_{res}$ (t)	65	6698.78	5446.49	7.25	0.02
7A	M (t) / B1 (t)/ B2 (T)	M_{tr} (t) /+/ $B1_{tr}$ (t) /+/ M_{res} (t) /+/ $B1_{res}$ (t) = $B2_{res}$ (t)	43	6747.61	5441.25	2.00	0.21
8A	**M (t) / B1 (t)/ B2 (T)**	**M_{tr} (t) = $B1_{tr}$ (t) /+/ M_{res} (t) /+/ $B1_{res}$ (t) = $B2_{res}$ (t)**	**42**	**6747.61**	**5439.25**	**0.00**	**0.58**
9A	M (t) / B1 (t)/ B2 (T)	M_{tr} (t) = $B1_{tr}$ (t) /+/ M_{res} (t) /+/ $B1_{res}$ (t) /+/$B2_{res}$ (t)	43	6748.626	5442.05	2.80	0.14
10A	M (t) / B1 (t)/ B2 (T)	M_{tr} (t) = $B1_{tr}$ (t) /+/ M_{res} (t) = $B1_{res}$ (t) = $B2_{res}$ (t)	41	6808.58	5485.64	46.39	0.00
11A	M (t) / B1 (t)/ B2 (T)	M_{tr} = $B1_{tr}$ / M_{res} / $B1_{res}$ = $B2_{res}$	29	6863.74	5505.41	66.17	0.00

Survival was modelled by contrasting models in which survival probability varied over time (models 1A to 6A; Table 2), in parallel among colonies, i.e. no interaction between colonies and time (models 7A to 9A; Table 2), and was constant over time and/or colonies (models 10A and 11A; Table 2). Akaike weights showed that models without the interaction term between time and colony were more plausible (models 7A to 9A; Table 2). We then tested for the effect of colony on survival of both newly marked (models 3A, 6A and 8A to 11A; Table 2) and resident birds, at large (i.e. Benidorm vs. Marettimo, models 4A and 10A; Table 2) and small scales (i.e. Cave 1 vs. Cave 2 at Benidorm, models 5A to 8A and 10A; Table 2). A model with a parallel variation over time in survival probabilities between newly marked and residents birds, no differences between newly marked birds at Benidorm and Marettimo and no differences between residents in Caves 1 and 2 from Benidorm (model 8A; Table 2) was retained as the most plausible model (w=0.58). Evidence ratios showed that this model was tied with model 7A, which included differences in survival probabilities between newly marked birds at Marettimo and Benidorm, and model 9A which included differences in survival probabilities between residents at all colonies (Table 2). Model averaged estimates showed that local survival for newly marked birds at Marettimo and Benidorm was similar (Fig 3b) and resident survival probability was higher at Marettimo than at Benidorm, where survival were similar between caves (Fig 3c). Models without a colony effect (model 10A, Table 2) or an effect of time (model 11A; Table 2) on survival were not retained.

Breeding success and sex ratio at fledging in Benidorm Island

The effects of age and colony on breeding success were modelled from the breeding output of birds marked as fledglings (models 1 to 14; Table 3a). The highest Akaike weight was from a model in which the breeding success varied in parallel between colonies as a function of age until age 4 (model 4; Table 3a). Nevertheless, evidence ratios showed that this model was only 1.14 times more likely than a model without a colony effect (model 3; Table 3a) and tied for the best model status with all other models with the exception of models 11 and 14 (Table 3a). The average (and SE) breeding success was 0.53 (0.05) (model 1; Table 3a), 0.50 (0.06) and 0.57 (0.07) in Caves 1 and 2 respectively (model 2; Table 3a). Model averaged estimates from

GLM mixed models (models 1 to 14, Table 3a,b) indicated that birds less than 4 years old had a lower breeding success than older birds (Table 3b). The breeding success of birds aged 4, 5 and older was very similar (Table 3b). Results from sex ratio Bayesian analysis showed that the proportion of males was 0.56 (95% credible interval 0.46-0.66) and that the sex ratio of fledglings was slightly male biased (the posterior probability of the proportion of males being larger than 0.5 was 0.90).

TABLE 3. a) Modelling age- and colony-dependent variation in the breeding success at Caves 1 and 2 at Benidorm Island, Spain, noted B1 and B2. Notation as in Table 1. Note that 3 years old was the earliest age of first reproduction at Benidorm colonies. Model with the higher w_i is in bold. **b**) Age-dependent breeding success estimates and standard error of European storm petrel marked as fledglings and subsequently breeding at Benidorm Island obtained though model averaging.

a)

Model	breeding success	np	dev	QAICc	ΔQAICc	w_i
1	B1=B2	1	165.80	169.80	3.20	0.05
2	B1/B2	2	165.20	171.20	4.60	0.02
3	B1 a(3,4:13) = B2 a(3,4:13)	2	160.80	166.80	0.20	0.21
4	**B1 a(3,4:13) /+/ B2 a(3,4:13)**	**3**	**159.60**	**166.60**	**0.00**	**0.24**
5	B1 a(3,4:13) / B2 a(3,4:13)	4	157.70	167.70	1.10	0.14
6	B1 a(3_4,5:13) = B2 a(3_4,5:13)	3	160.70	168.70	2.10	0.08
7	B1 a(3_4,5:13) /+/ B2 a(3_4,5:13)	4	158.60	168.60	2.00	0.09
8	B1 a(3_4,5:13) / B2 a(3_4,5:13)	6	157.40	171.40	4.80	0.02
9	B1 a(3_5,6:13) = B2 a(3_5,6:13)	4	159.60	169.60	3.00	0.05
10	B1 a(3_5,6:13) /+/ B2 a(3_5,6:13)	5	157.60	169.60	3.00	0.05
11	B1 a(3_5,6:13) / B2 a(3_5,6:13)	8	155.90	173.90	7.30	0.01
12	B1 a(3_6,7:13) = B2 a(3_6,7:13)	5	159.50	171.50	4.90	0.02
13	B1 a(3_6,7:13) /+/ B2 a(3_6,7:13)	6	157.50	171.50	4.90	0.02
14	B1 a(3_6,7:13) / B2 a(3_6,7:13)	10	155.40	177.40	10.8	0.00

b)

Colony	Age	Breeding success	SE
Cave 1	3	0.22	0.07
Cave 1	4	0.56	0.07
Cave 1	5	0.56	0.07
Cave 1	6-13	0.54	0.06
Cave 2	3	0.31	0.11
Cave 2	4	0.59	0.08
Cave 2	5	0.60	0.07
Cave 2	6-13	0.58	0.06

Population matrix modelling

Projections from population models indicated contrasting trends among the colonies, although the differences between the long-term deterministic growth rates were not statistically significant due to the large 95% confidence intervals (mean (and SE): 0.89 (0.05), 0.98 (0.03), 0.97 (0.04) for Cave 1, Cave 2 and Marettimo, respectively). Surprisingly, the different combinations of recruitment, survival and breeding success estimates from the three colonies led to similar population growth rates (respecting confidence intervals). Estimates for Marettimo and Cave 2 were not statistically different from a stable population, i.e. λ=1 (p=0.45 and p=51, respectively). Parameter estimates from Cave 1 were not high enough to reach stability (p=0.03). The population growth rate at all colonies showed the greatest sensitivity to changes in adult survival (Table A2, see Appendix II). The highest sensitivity was to survival of birds aged more than 5 years (sensitivity=0.69, 0.85 and 0.80 for Marettimo, Cave 1 and Cave 2 respectively). As predicted from life-history theory, sensitivity to juvenile survival and fertility was low in all colonies. As data on breeding success for Marettimo colony was not available, and in order to avoid parameter borrowing from Cave 2, we performed a new matrix model (results not shown) in which breeding success at Marettimo for birds aged 1 and 2 was fixed to 0 and breeding success for older birds was fixed to 0.3 (a value in the low boundaries for this species in absence of perturbations caused by high predation). The lambda value obtained under this scenario was 0.933 (S.E.=0.035). As sensitivities for fertility were small, results did not change substantially. Estimated population growth rate was not different from a stable population (p=0.056).

DISCUSSION

Provided herein are the first age-dependent estimates of survival, recruitment and breeding success for the vulnerable European storm petrel from three colonies in the Mediterranean basin. Robust estimates of demographic parameters are necessary for a conservation diagnosis of threatened species or populations and to provide guidelines for management actions (Morris & Doak 2002). In addition, the hypogeous nesting habit of the species makes it difficult to obtain reliable estimates

of population size and population dynamics can only be approached by means of individual-based demographic data (Oro et al. 2004b).

Our results showed important similarities between colonies, but also differences in recruitment processes and survival probabilities. As expected, the analyses of birds marked as fledglings indicated that survival, recruitment and breeding success probabilities increased with age. In agreement with the general findings on long-lived birds, youngest individuals had a low breeding success and showed a low local survival (Forslund & Pärt 1995, Tavecchia et al. 2001, Breton et al. 2006). At present, we do not know if the low survival by the youngest birds resulted from natal dispersal or mortality, since capture-recapture models do not distinguish these two possibilities without additional information, e.g. recoveries of dead birds (Lebreton et al. 1992, Breton et al. 2006). Accession to reproduction (recruitment) varied among colonies: in Marettimo birds began to reproduce earlier than in the other two colonies but the full recruitment was attained later. We do not have an explanation for these differences: a first cause may be a difference in predatory pressure among the colonies which may have delayed accession to reproduction in young inexperienced prospectors (Rood & Reznick 1997, Oro et al. 2005). This would explain why in the colony where predation by yellow legged gulls was high individuals tended to recruit later, but it would not explain why in this colony the full recruitment was attained faster than Marettimo, where predation was thought to be very low. A further possible cause is that suitable breeding sites may not be equally available due to differences in density-dependence at each colony (Frederiksen et al. 2005, Tavecchia et al. 2008) affected by the existence of artificial nest-boxes at Benidorm. A third possible, non-exclusive explanation is that food resources are more abundant around Marettimo leading to improved body conditions relative to Benidorm and earlier recruitment, but at the moment we have no data to support this hypothesis.

Birds marked as fledglings (older than 2 years old at Marettimo and 3 at Benidorm) clearly had a higher average survival probability than birds marked as adults. This reflects the yearly variation in survival and the temporal window of the analysis. Data from birds marked as fledglings came mainly from the last 4-6 years of the study

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when the probability of survival was higher (Fig 3), especially at Benidorm Island where in those years a selective culling program on yellow legged gulls was carried out to reduce predation pressure (Sanz et al. 2005, Sanz-Aguilar et al. 2009a). Survival probabilities of birds marked as adults varied over time (not assessed in analysis of birds marked as fledglings) and among colonies, the exception being the survival of birds in Caves 1 and 2 at Benidorm (narrow spatial scale), which appeared to be similar in all years. However difference between Marettimo and Benidorm (broad spatial scale) seemed to disappear near the end of the study when survival was similar among colonies (Fig 3). These and published results (Oro et al. 2005, Tavecchia et al. 2008, Sanz-Aguilar et al. 2009a) suggest that predation by yellow legged gulls may be the principal factor influencing differences in survival among colonies in this long-lived species. Other factors such as climatic conditions or food availability around the colonies or in the wintering grounds could generate differential additive mortality between the Italian and the Spanish colonies (Frederiksen et al. 2005).

Population models suggested that different age-dependent patterns of demographic parameters can lead to similar population growth rates. This is the case, for example, between the colony of Marettimo (where birds attained full recruitment the latest but started to reproduce the earliest) and Cave 2 at Benidorm (where birds recruited later but experienced a slightly higher local survival). In both cases, long-term model projections indicated a stable population, whereas the model from Cave 1 at Benidorm (where predation was higher and the buffering mechanisms limited, see Ferrer et al. 2004, Grimm et al. 2005) indicated a declining trend. The difference in population growth rates was mainly caused by adult survival rather than by patterns of recruitment, to which population growth rate had a lower sensitivity. And as reflected in this result, the most sensitive parameter in terms of population growth rate was adult survival, in accordance with evidence on other studies from long-lived organisms (Saether & Bake 2000).

The greater variability was also found in the parameter that less influences average individual fitness: the highest population growth rates were found at the colonies with the highest survival even though they had different recruitment patterns. Our population matrix models were built using data from birds marked as fledglings that

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recruited at the end of the study when survival was generally high, at least at Benidorm, because the predation by the yellow-legged-gull was experimentally reduced (Sanz-Aguilar et al. 2009a). In this respect our model describes an optimistic scenario as average value of survival before the experiment was probably lower. It may be possible that under high predation pressure of the yellow legged gull, storm petrel populations are likely to go extinct in the long term due to reduction in adult survival probabilities. In fact, results indicate a declining trend in the Cave 1 population, although this decline might be buffered by immigration, which was not considered in the model, or by management actions designed to enhance petrel's adult survival, like the periodic removal of specialist gulls (Oro et al. 2005, Sanz et al. 2005, Sanz-Aguilar et al. 2009a). Further studies should focus on environmental predictors (e.g. predation pressure, food and nest-site availability) of demographical traits and immigration-emigration mechanisms at metapopulation scale to be able to set up conservation actions at large geographical scales (Breton et al. 2006).

The goodness-of-fit test of the general Cormark-Jolly-Seber capture-recapture model

Under the assumption that individuals share the same parameters, i.e. the homogeneity assumption, the distribution of individual encounter histories can be written as a combination of two probabilities: the probability that an individual survives the interval i to $i+1$ (i.e. the survival probability at i, generally noted Φ_i) and the probability that an individual known to be alive, is caught, or seen, at $i+1$ (i.e. the recapture probability at $i+1$, denoted p_{i+1}). The goodness-of-fit test of homogeneity deployed here is divided into four different sets of contingency tables, that help to identify whether the survival (mainly tests 3.SR and 3.SM,) or recapture processes (mainly test 2.CT and 2.CL) depend on an individual encounter history (see also Tavecchia et al. 2007). The component 3SR assesses, in particular, if the survival probability after marking is different from subsequent survival probabilities. In birds marked as fledglings, this is equivalent to a test of age-dependence in local survival while in adult birds this is a test for the presence of transient animals, i.e. birds seen only at marking and never seen after (Pradel et al. 1997). The results of the homogeneity goodness-of-fit tests based on a model in which all parameters are time dependent, i.e. the Cormark- Jolly Seber model (CJS), are shown for birds marked as adults and as fledglings in Table A1. A variance inflation factor, $\hat{c}$, for the general Cormark-Jolly-Seber model can be calculated as follows:

$$\hat{c} = \frac{\sum\limits_{groups} \chi^2 (3.SR + 3.SM + 2.CT + 2.CL)}{\sum\limits_{groups} df (3.SR + 3.SM + 2.CT + 2.CL)}$$

If test 3.SR is significant, model selection should begin from a model including specific parameters for the survival of newly marked animals (Pradel et al. 1997); and c-hat should be calculated for this new model as follows:

$$\widehat{c} = \frac{\sum\limits_{groups} \chi^2 \, (3.SM + 2.CT + 2.CL)}{\sum\limits_{groups} df \, (3.SM + 2.CT + 2.CL)}$$

This is the starting model that we developed in our capture-mark-recapture analysis of birds marked as adults; and this model without time for birds marked as fledglings.

TABLE A1. Testing assumptions of the Cormark-Jolly Seber model, including time- and group-dependent parameters for birds at Marettimo 'M' and at Benidorm ('B1' and 'B2' for birds marked at Cave 1 and 2, respectively). Significant chi-square statistics (p<0.05) are in bold.

Goodness-of-fit components	M		B1		B2	
	χ^2	np	χ^2	np	χ^2	np
Birds marked as fledglings						
3.SR *transient effect*	**70.25**	**11**	**96.35**	**9**	**81.29**	**6**
3.SM	11.20	8	13.38	7	6.61	4
2.CT *trap-dependence effect*	17.27	10	12.87	7	4.47	6
2.CL	**30.02**	**16**	3.24	8	9.79	9
Total	**128.73**	**45**	**125.84**	**31**	**102.12**	**25**
Birds marked as adults						
3.SR *transient effect*	**37.26**	**11**	**42.35**	**12**	19.03	11
3.SM	16.57	17	8.34	11	15.44	10
2.CT *trap-dependence effect*	**16.79**	**8**	**27.01**	**11**	8.92	10
2.CL	19.78	24	8.54	8	6.98	7
Total	**90.41**	**60**	**86.24**	**42**	50.35	38

APPENDIX II

Population Matrix Modelling

If $\mathbf{N}_i$ is a vector containing the number of birds in the *n* age classes at occasion *i*, the population at *i*+1 is $\mathbf{N}_{i+1}=\mathbf{A}\ \mathbf{N}_i$ (Caswell 2001), the matrix A is denoted as the transition matrix and contains the *n*-age-dependent parameters where *n* is the number of age classes necessary to describe the focal species life-cycle (in our case n=6; Table A2). The matrix **A** takes the form:

$$
\mathbf{A}=\begin{bmatrix}
\phi_1\pi_1 F_1 & \phi_2\pi_2 F_2 & .... & \phi_n\pi_n F_n \\
\phi_1 & 0 & ... & 0 \\
0 & \phi_2 & ... & 0 \\
0 & 0 & ... & 0 \\
0 & 0 & ... & \phi_n
\end{bmatrix}
$$

Where:

Φ_j = the average survival of birds from age j-1 to age j

π_j = proportion of birds breeding at age *j*

F_j = the average number of female fledglings per breeding female

$B_j = (\Phi_j\ \pi_j\ F_j)$ the number of females born per breeding female of age *j*

Here, the vector $\mathbf{N}_i$ is unknown but the matrix formulation permits to estimate the asymptotic population growth, λ, as the dominant eigenvalue of **A**. In a stable population the population growth rate is equal to 1. Lower values indicate a decreasing trend. The 95% confidence interval of λ can be estimated by combining parameter variance and sensitivity (Lande 1988b).

Perturbation analyses permit the investigation of the sensitivity of the population growth rate to each entry in the matrix **A** (Caswell 2000). The sensitivity analysis gives an indication of how a change of a specific parameter affects the population growth rate. Note that in our case not all parameters were available for each colony. The breeding success in Marettimo, for example, was not available and was assumed to be similar to Cave 2 from Benidorm which experienced the lower predation pressure relative to Cave 1 over the study period (Table A2).

TABLE A2. Age- and colony-dependent estimates (se) of demographic parameters and sensitivity of matrix model entries. Fertility is the number of females born per breeding female of age j (see matrix A).

Colony	Age	Survival	Sensitivity Survival	Breeding proportion	Breeding success	Fertility	Sensitivity Fertility
Marettimo	1	0.57 (0.05)	0.110	0.07 (0.02)	0.30 (0.11)	0.005 (0.003)	0.065
	2	0.57 (0.05)	0.109	0.15 (0.03)	0.30 (0.11)	0.012 (0.005)	0.038
	3	0.89 (0.03)	0.068	0.65 (0.07)	0.30 (0.11)	0.076 (0.031)	0.023
	4	0.89 (0.03)	0.064	0.64 (0.08)	0.62 (0.08)	0.155 (0.034)	0.021
	5	0.89 (0.03)	0.059	1	0.62 (0.08)	0.243 (0.047)	0.019
	6	0.89 (0.03)	**0.685**	1	0.60 (0.07)	0.235 (0.044)	0.223
Benidorm (Cave 1)	1	0.47 (0.04)	0.057	0	0	0	0
	2	0.47 (0.04)	0.057	0	0	0	0
	3	0.47 (0.04)	0.057	0.11 (0.06)	0.21 (0.09)	0.005 (0.003)	0.008
	4	0.86 (0.04)	0.030	0.92 (0.16)	0.54 (0.08)	0.188 (0.098)	0.049
	5	0.86 (0.04)	0.029	1	0.55 (0.07)	0.208 (0.050)	0.004
	6	0.86 (0.04)	**0.850**	1	0.53 (0.06)	0.201 (0.047)	0.125
Benidorm (Cave 2)	1	0.55 (0.03)	0.073	0	0	0	0
	2	0.55 (0.03)	0.073	0	0	0	0
	3	0.55 (0.03)	0.071	0.97 (0.14)	0.30 (0.11)	0.070 (0.029)	0.013
	4	0.94 (0.02)	0.040	1	0.62 (0.08)	0.256 (0.057)	0.007
	5	0.94 (0.02)	0.038	1	0.62 (0.08)	0.256 (0.057)	0.007
	6	0.94 (0.02)	**0.801**	1	0.60 (0.07)	0.248 (0.054)	0.143

CAPÍTULO 3

THE COST OF REPRODUCTION AND EXPERIENCE-DEPENDENT VITAL RATES IN A SMALL PETREL

The cost of reproduction and experience-dependent vital rates in a small petrel

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ABSTRACT

Life history theory predicts that higher levels of reproductive investment entail higher reproductive costs especially among young and inexperienced individuals that might not optimize reproductive investment. Using a long-term individual and state-dependent capture-recapture data on Storm petrels (*Hydrobates pelagicus)* we analyzed whether breeding experience and current breeding investment were associated with the expression of the cost of reproduction in terms of reduced survival and/or future breeding performance. We found a positive relationship between current breeding investment, breeding experience and future survival and an improvement in breeding performance with individual experience independently of the previous breeding outcome. Our results suggest that the survival cost paid by first-time breeders and the positive correlation between reproduction and survival corresponds to a selection against low quality birds unrelated with the breeding effort. Our work outlined the need to investigate the effect of multiple individual traits on different life-history trade-offs simultaneously.

Keywords: breeding experience; breeding success; demography; multistate capture-recapture analysis; Procellariiformes; reproductive cost; survival probability.

INTRODUCTION

Trade-offs, defined as the negative correlations between traits that constrain their simultaneous evolution, constitute one of the central topics in the life history theory (Fox et al. 2001). Such theory postulates the cost of reproduction hypothesis, which predicts a negative covariation between the effort in the current reproduction and the future survival and/or fecundity (Stearns 1992, Roff 1992, McNamara & Houston 1996). In long-lived species, in which individual fitness is dominated by the high survival rate, a cost of reproduction is expected to be evident on fecundity and not on future survival (Roff 1992, Crone 2001). An extreme example are the long-lived seabirds of the order Procellariiformes that are characterized by very high annual adult survival rates, deferred breeding and low reproductive output (Warham 1990,

Warham 1996). In these species the population growth rate is highly sensitive to small changes of adult survival probability (Saether & Bakke 2000). Moreover, it has been suggested that parental effort in Procellariiformes is regulated to a fixed investment, independently of offspring needs (Navarro & González-Solís 2007). Potential costs of reproduction are thus expected to be buffered by adjustments in current breeding performance through, for example, reproductive skipping or nest desertion during adverse environmental conditions (Erikstad et al. 1998, Wernham & Bryant 1998, Orzack & Tuljapurkar 2001, Jenouvrier et al. 2005).

Because optimal reproductive investment can mask the negative correlation between traits, evidence of the cost of reproduction is generally derived from experimental studies in which individuals are forced to increase or reduce their current reproductive investment (Reznick 1985, Reznick 1992, Stevenson & Bancroft 1995, but see Doligez et al. 2002). In non-manipulative studies, reproductive costs may not be visible because individuals would invest according to their resources or intrinsic quality (Van Noordwijk & Dejong 1986, Erikstad et al. 1998, Reznick et al. 2000) leading to positive correlations between fitness components at the population level, i.e. the selection hypothesis (Cam & Monnat 2000, Cam et al. 2002, Mauck et al. 2004, Blums et al. 2005, Tavecchia et al. 2005, Barbraud & Weimerskirch 2006). Nonetheless, in some cases, long-term correlative studies based on detailed information on a sufficiently large number of individuals, provide evidence of a reproductive cost (Moyes et al. 2006), typically under severe environmental conditions (Tavecchia et al. 2005, Nevoux et al. 2007), during the first-breeding attempt (Cam & Monnat 2000, Barbraud & Weimerskirch 2005), or in the first years of life (Tavecchia et al. 2001).

The first-breeding attempt in particular has been shown to be a critical period during which a cost of reproduction may be evident (Cam & Monnat 2000). In fact, first-time breeders have regularly been shown to exhibit a lower probability of breeding successfully (Weimerskirch 1990, Barbraud & Weimerskirch 2006, Nevoux et al. 2007), a lower local survival or return rate than experienced breeders (Pyle et al. 1997, Bradley et al. 2000, Barbraud & Weimerskirch 2005, Nevoux et al. 2007) and a higher probability of non-breeding the following year (Coulson & Thomas 1985,

Weimerskirch 1990, Viallefont et al. 1995, Cam & Monnat 2000, Barbraud & Weimerskirch 2005). At individual level these costs can be mediated by metabolic and regulatory signals triggered by the first reproduction (Harshman & Zera 2007) or simply by a lack of breeding experience, i.e. partner bond or ability to sustain long incubation periods (i.e. the breeding experience hypothesis, Ollason & Dunnet 1988, Bradley et al. 2000). However, first-time breeders are on average younger than experienced breeders, and both lack of breeding experience and age can affect individuals simultaneously (Cam & Monnat 2000, Bradley et al. 2000, Tavecchia et al. 2001, Ratcliffe et al. 2002, Reid et al. 2003, Moyes et al. 2006). There are clearly strong challenges to studying the cost of reproduction from correlative studies. For example, in trying to separate the effects of experience from that of age, one ideally needs the complete information on the past breeding attempts of known-aged individuals. This information is obviously rarely found, especially for a large number of individuals. Also, in natural populations the probability of detection needs to be taken into account to obtain unbiased estimate of survival and other similar demographic parameters (Boulinier et al. 1997).

Here we analyze 1) the experience-dependent cost of reproduction in terms of breeding performance at individual level, and 2) future survival and future reproduction at population level in the European storm petrel *Hydrobates pelagicus*. Storm petrels are a small (average weight 28g) and long-lived Procellariiformes seabird with an extended breeding period (incubation lasts about 40 days and chick rearing about 63-70 days). They lay a single and proportionally large egg (ca. 30% of adult body mass) and their chicks reach a body mass ca. 130% that of adults (Warham 1990, Mínguez 1996, Mínguez 1998). Their breeding effort invested in natural conditions is potentially costly and suitable to evaluate the trade-off between reproductive investment and survival. We used a long-term detailed stratified data and multistate capture-recapture models to measure the influence of the current reproduction on future survival and fecundity by modeling simultaneously survival, between-states transitions and detection probability (Nichols et al. 1994, Nichols & Kendall 1995). Such models are suitable to test how survival and future breeding probability change according to the current breeding investment in the context of capture-recapture studies where observations are incomplete (Nichols & Kendall

1995). At the moment, this type of models can not take into account the difference in intrinsic quality among individuals but, if individual heterogeneity may mask or reduce the observed magnitude of the tradeoff, it cannot fake it. Hence, in correlative studies, the absence of a correlation between traits cannot be considered as a strongly supports for their independence, but a negative correlation is an indication of a phenotypic link between the traits (Nur 1988).

METHODS

Study area

The study was conducted at Benidorm Island, a 6.5ha Special Protection Area for the conservation of the European storm petrel, in the Mediterranean coast of Spain (38° 30'N, 0° 08'E). Here breeding petrels concentrate in two caves where they nest at high densities. One colony (cave 1, hereafter) contains over 200 breeding pairs whereas the other colony (cave 2, hereafter) is home to approximately 100 breeding pairs (Mínguez 1994). In 1996, a number of artificial nest-boxes were installed inside both colonies but they were principally occupied in cave 2 only (de León & Mínguez 2003). Each year, breeding birds were caught only once, during the incubation period. However, each nest was inspected at least four times during the whole breeding period to record individual breeding success. Breeding adults caught in their nest were marked with stainless steel rings with a unique alphanumeric code. No ring degradation was ever recorded and we assumed that metal ring loss is negligible.

Stratified observations

We considered 1657 observations of 639 breeding birds captured in their nests during the period 1994-2006 in cave 1 and during 1995-2006 in cave 2. Observations were first classified according to individual known breeding experience. Individuals captured for the first time in nests monitored in previous occasions were classified as 'first-time breeders' ('FTB' hereafter), whereas individuals previously recorded as breeders were classified as experienced breeders ('EB' hereafter). Observations on individuals captured for the first time in nests that were not monitored previously

were discarded. As found in other studies, the breeding tenacity was extremely high and only 12 birds have changed nest during the study period. For this reason birds were unlikely to be missed as a consequence of local breeding dispersal. Breeding dispersal to the other colony was also very rare and individuals caught in one colony have never been observed in the other one, with the exception of one case (deleted in the current analysis). Nonetheless, there are instances when a nest was known to be occupied but the bird has not been captured. Thus, capture failures were not necessarily associated with empty nests. To summarize, breeding dispersal and reproductive skipping were negligible in both colonies, consequently, recapture probability does not reflect breeding frequency. Note that here immature animals, i.e. individuals that have not bred yet, were never considered. Observations of breeding birds were stratified in 'unsuccessful' or 'successful', according to the breeding success at the end of the current breeding occasion. Individuals failing to hatch or to rear a chick were considered unsuccessful. The breeding success was considered as an individual state allowing transitions between its two levels at any time interval. Individuals were also classified in relation to the breeding colony (cave 1 or cave 2), but no movements between these two levels were allowed. Each individual first caught as first-time breeder became automatically experienced breeder in the next occasion so that animals do not remain first-time breeder from more than one occasion.

Statistical analysis and model notation

Current breeding success.— The effect of experience on the current breeding success was examined using generalized linear mixed models (McCulloch & Searle 2001). We analyzed a total of 1657 breeding outcomes, 288 of which from first-time breeders. The breeding output was treated as a binary variable (1=successful, 0=unsuccessful) and modeled as a function of bird experience using the glmmML function in the statistical package R (www.R-project.org/). The individual identity was treated as a random effect to control for multiple contributions made by the same individual.

Survival and future breeding success.— We evaluated the influence of the colony, individual breeding experience and current breeding success state on survival and

future breeding success probabilities. To do this, observations were written in multistate encounter-histories and analyzed using multistate capture–recapture models (Brownie et al. 1993, Lebreton & Pradel 2002) with the program M-SURGE (Choquet et al. 2004). These models include three types of parameters for each colony (Nichols et al. 1994), noted and defined as follows:

- p_{rt} : the probability that a marked bird is recaptured at time t in state r, given that it is alive and present in the population at time t. The two possible states are unsuccessful and successful breeder.

- Φ_{rt}: the probability that a bird in state r at time t survives until t + 1.

- Ψ_{rst} : the probability that a bird in state r at time t is in state s at t+1, given that the individual survived from time t to time t + 1. Note that this probability is conditional to survival.

These three parameters were estimated simultaneously from encounter histories by maximum likelihood procedure (Choquet et al. 2004). Program M-SURGE additionally provides automatically the model rank, i.e. the number of separately identifiable parameters, and accounts for the rank and data to compute the Akaike's Information Criterion (Choquet et al. 2004). The non-identifiable parameters are also listed individually. Multistate models do not distinguish mortality from permanent emigration and survival should be considered as local (Lebreton et al. 1992). The general model we began with is equivalent to the traditional Arnason-Schwarz model (Schwarz et al. 1993) extended to two groups, i.e. colony 1 and 2 , and with two apparent " age classes", i.e. first-time and experienced breeder. We began to model recapture, survival and transitions processes by the general model ($p_{t*cave*bs}$, $\Phi_{t*exp*bs*cave}$, $\Psi_{bs*t*exp*cave}$) assuming for survival, Φ, and transition, Ψ, probabilities an effect of the colony, noted "cave", the year, noted "t", the experience, noted "exp" and the breeding success state, noted "bs". In this model the probability of recapture, p, varied according to the colony, the year, and the breeding success state. We refer to this general model as the "umbrella model". The goodness of fit of the umbrella model was assessed through contingency tables using program U-CARE 2.2.2 (Pradel et al. 2003, Choquet et al. 2005). The effect of the experience was not considered in the umbrella model nor in any other model as predictor of p because this parameters refers to the recapture probability of birds after the marking and by

this time first-time breeders have become experienced breeders. Note also that most captures occurred during the incubation period when failed breeders were still present; consequently the breeding success cannot be associated with the recapture probability. It was however included in the umbrella model because the only goodness of fit test available is for a model including all effects on all parameters, i.e. the umbrella model. Model selection was based on Akaike Information Criterion (AIC) and the Akaike weights (w_i, for each model i) were calculated as an index of the relative plausibility of each model. Estimates of Φ and Ψ were obtained by model averaging in which each model contributed to the final estimate according to its Akaike weight (Burnham & Anderson 2000). The importance of a particular effect can be refined by making inference from all models in the candidate set. Akaike weights, w, were summed for all models containing the effect considered. The effect with the largest sum of w, denoted w+, was considered to be the most important (Burnham & Anderson 2000). Model selection proceeded as follows. We first simplified the structure of p keeping the structure of Φ and Ψ as general as possible, i.e. as in the umbrella model. Subsequently we retained the selected structure of p and conducted two separate model selection processes for Φ and Ψ, respectively (Grosbois & Tavecchia 2002). Here we kept the structure of the parameter that was not modeled as in the umbrella model. For example, when modeling survival, transition probabilities were assumed to vary as a function of all effects considered. This procedure minimized the bias resulting from the order in which we modeled each parameter (i.e. survival and future breeding success probabilities, Hadley et al. 2007).

RESULTS

Current reproductive success

The model including the experience as predictor of the current success was highly preferred over a model with no effect of experience (model 1, Table 1). According to this model the breeding success of the first observed breeding attempt was ca. 10% lower than in subsequent years (46.9% and 59.3%, respectively).

TABLE 1. The role of the breeding experience and age in the breeding success of European storm petrels at Benidorm Island (western Mediterranean). The subscripts 'FTB' and 'EB' denoted the effect of the breeding experience and its two levels, first-time breeder and experienced breeder, respectively. When no effects were considered (i.e. a constant value) the symbol '.' was used in model notation. Abbreviations are: np, number of parameters; Dev, relative deviance; AIC, Akaike information criterion; Δ_i, the AIC difference between the current and lowest AIC model; w_i, Akaike weigth. The retained model is in bold.

Modelling the effect of experience in current breeding success						
Model	Effect	np	Dev	AIC	Δ_i	w_i
1	**FTB, EB**	**2**	**2241**	**2247**	**0**	**0.998**
2	.	1	2256	2260	13	0.002

Survival and future reproductive success

The umbrella model (model U, Table 2) explained the data adequately (goodness-of-fit test: $\chi^2 = 248.737$, df = 293, $P = 0.973$). A more realistic model without the effect of breeding success in the probability of recapture was preferred (Table 2). In agreement with a previous study (Tavecchia et al. 2008) we found that recapture probability was high and varied over time in both colonies. In cave 2 it increased linearly over time due to the progressive occupancy of artificial nest-boxes (model 3, Table2, Fig. 1, Tavecchia et al. 2008).
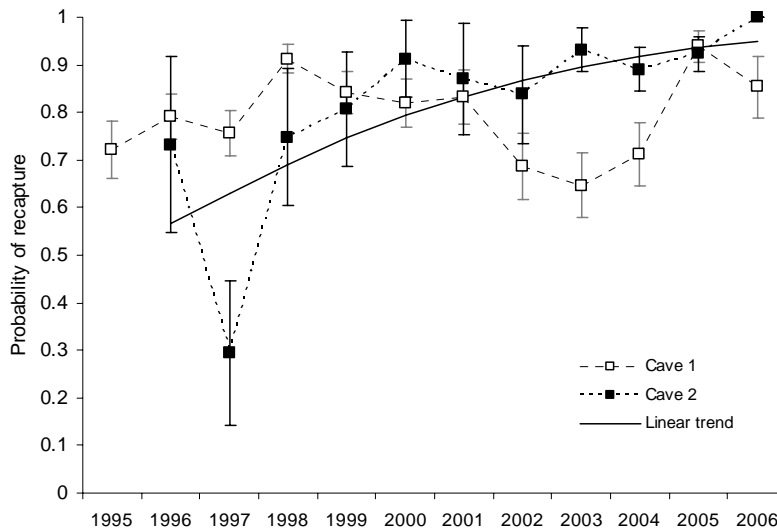
FIGURE 1. Average annual estimates (± SE) of recapture probabilities of European storm petrels breeding in cave 1 (empty symbols) and cave 2 (full symbols) at Benidorm Island, western Mediterranean. Estimates are form models assuming a linear trend in cave 2 (solid line) and a full time effect in cave 1 (models 31, 32 and 33, Table 2).

TABLE 2. Estimation of recapture, survival and future breeding probabilities of European storm petrels breeding at Benidorm Island (western Mediterranean) by multistate capture-recapture modeling. The effects considered were yearly variation (denoted 't'), linear variation in time (denoted 'lvt'), colony (denoted 'cave', 'c1' and 'c2' for the two levels, colony 1 and 2, respectively), breeding experience (denoted 'exp', 'FTB' and 'EB' for the two levels, first-time breeders and experienced breeders respectively) and the breeding success (denoted 'bs'). The symbol '*' was used to denote the statistical interaction between the effects. In models without an interaction effect (i.e. parallel variation), the symbol '+' was used instead. When no effects were considered (i.e. a constant value) the symbol '.' is used in model notation. Abbreviations are: np, number of separately estimable parameters; Dev, relative deviance; AIC, Akaike information criterion; Δ_i, the AIC difference between the current and lowest AIC model; w_i, Akaike weigth. The retained models in each step of the analysis are in bold.

Model	Considered effects in P, Φ and ψ			np	Dev	AIC	Δ_i	w_i
	P	Φ	ψ					
Modelling recapture probabilities								
U	t*cave*bs	t*exp*bs*cave	bs*t*exp*cave	201	3361.82	3763.82	7.14	0.026
1	t*cave	t*exp*bs*cave	bs*t*exp*cave	183	3398.56	3764.58	7.90	0.018
2	t+cave	t*exp*bs*cave	bs*t*exp*cave	176	3414.76	3766.76	10.09	0.006
3	**t*c1, lvt*c2**	**t*exp*bs*cave**	**bs*t*exp*cave**	**176**	**3404.68**	**3756.68**	**0.00**	**0.931**
4	t	t*exp*bs*cave	bs*t*exp*cave	173	3418.89	3764.89	8.21	0.015
5	cave	t*exp*bs*cave	bs*t*exp*cave	163	3441.91	3767.91	11.23	0.003
Modelling survival probabilities								
6	t*c1, lvt*c2	t+exp+bs+cave	bs*t*exp*cave	114	3496.63	3724.63	4.90	0.041
7	t*c1, lvt*c2	t*exp*bs	bs*t*exp*cave	144	3461.13	3749.13	29.40	0.000
8	**t*c1, lvt*c2**	**t+exp+bs**	**bs*t*exp*cave**	**112**	**3496.97**	**3720.97**	**1.24**	**0.256**
9	**t*c1, lvt*c2**	**t+[exp*bs]**	**bs*t*exp*cave**	**113**	**3495.32**	**3721.32**	**1.59**	**0.215**
10	**t*c1, lvt*c2**	**t+FTB+[EB*bs]**	**bs*t*exp*cave**	**112**	**3495.70**	**3719.73**	**0.00**	**0.476**
11	t*c1, lvt*c2	t+EB+[FTB*bs]	bs*t*exp*cave	109	3511.52	3729.52	9.79	0.004
12	t*c1, lvt*c2	t+exp	bs*t*exp*cave	108	3511.90	3727.90	8.17	0.008
13	t*c1, lvt*c2	t+bs	bs*t*exp*cave	111	3513.18	3735.18	15.45	0.000
14	t*c1, lvt*c2	exp+bs	bs*t*exp*cave	101	3547.77	3749.77	30.04	0.000
Modelling future breeding success probabilities								
15	t*c1, lvt*c2	t*exp*bs*cave	bs*[t+exp+cave]	127	3496.85	3750.85	14.84	0.001
16	t*c1, lvt*c2	t*exp*bs*cave	bs*t*exp	143	3456.33	3742.33	6.33	0.037
17	t*c1, lvt*c2	t*exp*bs*cave	bs*[t+exp]	123	3507.06	3753.06	17.06	0.000
18	t*c1, lvt*c2	t*exp*bs*cave	bs+t+exp	111	3529.30	3751.30	15.30	0.000
19	t*c1, lvt*c2	t*exp*bs*cave	t*[FTB+EB*bs]	132	3483.05	3747.05	11.05	0.003
20	**t*c1, lvt*c2**	**t*exp*bs*cave**	**t*[EB+FTB*bs]**	**131**	**3474.00**	**3736.00**	**0.00**	**0.864**
21	t*c1, lvt*c2	t*exp*bs*cave	t+EB+FTB*bs	107	3531.97	3745.97	9.97	0.006
22	t*c1, lvt*c2	t*exp*bs*cave	bs*t	118	3509.80	3745.80	9.80	0.006
23	t*c1, lvt*c2	t*exp*bs*cave	bs+t	110	3531.62	3751.62	15.61	0.000
24	t*c1, lvt*c2	t*exp*bs*cave	bs*exp	101	3573.35	3775.35	39.35	0.000
25	t*c1, lvt*c2	t*exp*bs*cave	t*exp	120	3500.73	3740.73	4.72	0.081
26	t*c1, lvt*c2	t*exp*bs*cave	t+exp	110	3532.10	3752.10	16.09	0.000
27	t*c1, lvt*c2	t*exp*bs*cave	t	109	3534.09	3752.09	16.09	0.000
28	t*c1, lvt*c2	t*exp*bs*cave	exp	99	3577.71	3775.71	39.71	0.000
29	t*c1, lvt*c2	t*exp*bs*cave	bs	99	3579.24	3777.24	41.24	0.000
30	t*c1, lvt*c2	t*exp*bs*cave	.	98	3581.70	3777.70	41.69	0.000
Final models								
31	**t*c1, lvt*c2**	**t+exp+bs**	**t*[EB+FTB*bs]**	**62**	**3567.10**	**3691.10**	**1.08**	**0.286**
32	**t*c1, lvt*c2**	**t+[exp*bs]**	**t*[EB+FTB*bs]**	**63**	**3565.60**	**3691.60**	**1.58**	**0.223**
33	**t*c1, lvt*c2**	**t+FTB+[EB*bs]**	**t*[EB+FTB*bs]**	**62**	**3566.02**	**3690.015**	**0.000**	**0.491**
34	t*c1, lvt*c2	t+exp+bs	EB+FTB*bs	30	3669.65	3729.646	39.631	0.000
35	t*c1, lvt*c2	t+[exp*bs]	EB+FTB*bs	31	3668.10	3730.101	40.086	0.000
36	t*c1, lvt*c2	t+FTB+[EB*bs]	EB+FTB*bs	30	3668.49	3728.494	38.479	0.000
37	t*c1, lvt*c2	t+FTB+[EB*bs]	t+[exp*bs]	42	3645.08	3729.079	39.064	0.000

The modeling of survival probabilities retained time (w+=1), experience (w+=1) and breeding state (w+=0.99) effects as predictors of survival (models 8, 9, 10, Table 2). Such models included additive effects of time with experience and breeding success, i.e. parallel variation of survival over time among experience groups and breeding success states. Note that model 10 assumed a common survival parameter for first-time breeders regardless their current breeding success. Indeed the effect of current breeding success among first-time breeders was the least important predictor of future survival probability (w+=0.52). In future breeding success probabilities we retained the effects of time (w+=1), experience (w+=0.99) and of the current breeding success (w+=0.92). The effect of the current breeding success on transition probabilities was retained only for first-time breeders (w+=0.91) (model 20, Table 2) while among experienced breeders it was the least important predictor (w+= 0.05). At this stage, the selected structures of models 3, 8, 9, 10 and 20 were used to build the final models that considerably improved the AIC value (models 31, 32, 33, Table 2). According to these models (31 and 32 in Table 2), both the breeding experience and the breeding success had a positive effect on survival, although a simpler model without the effect of breeding success in first-time breeders was equally supported (model 33, Table 2). Annual averaged estimates of survival probabilities from models 31, 32 and 33 also indicated that current breeding success was not an important predictor for the survival of first-time breeders but it was for experienced breeders (Fig. 2). As for the future breeding success, averaged estimates showed that birds that survived had in general a high probability of breeding successfully the following year. Although confidence intervals overlap, the experience effect was retained by the selected models (Fig 3). Experienced breeders have the same probability of breeding successfully the subsequent year regardless of their current breeding output. This indicated that current effort in experienced birds does not influence future breeding outputs. In contrast the effect of the current breeding success, i.e. effort, was retained in first-time breeders although averaged estimates appeared very similar (Fig 3).
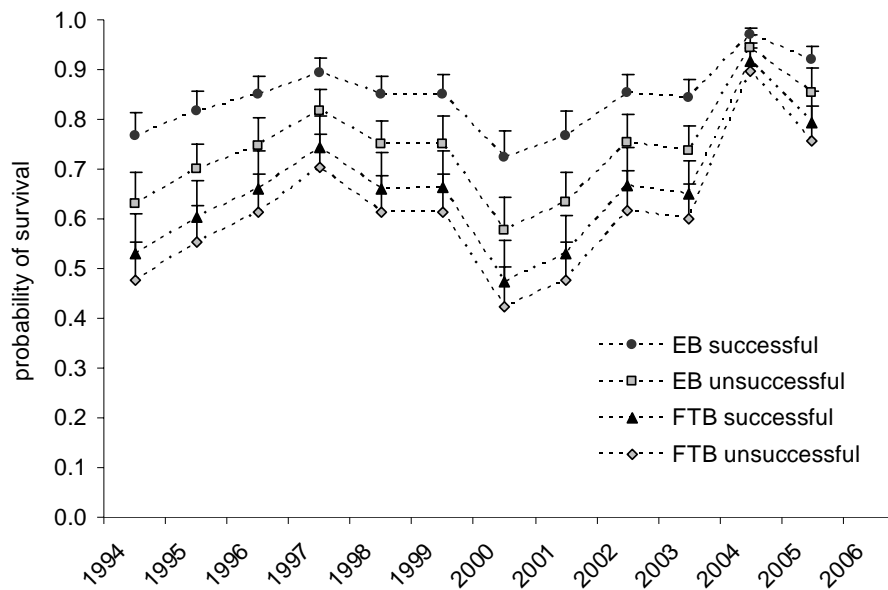
FIGURE 2. Annual variation in survival probability (+ or -1 SE) of European storm petrels averaged over models 31, 32 and 33 (see Table 2), in which survival varied among four groups: experienced and first-time breeders (EB and FTB respectively) with successful and unsuccessful birds.
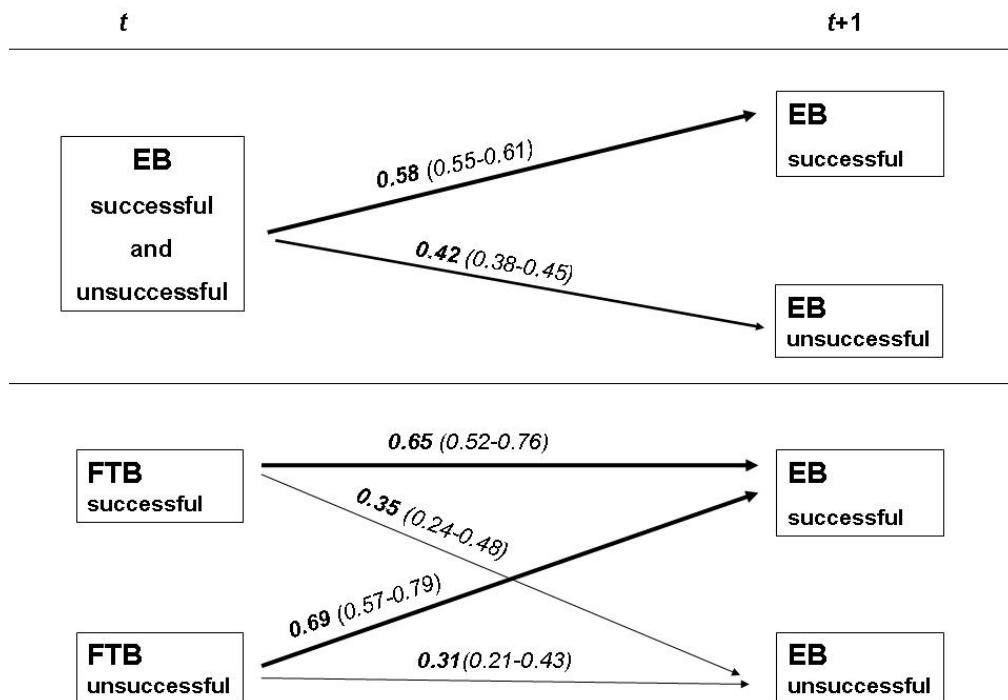
FIGURE 3. Estimates (95% confidence intervals in brackets) of future breeding performance transition probabilities. Transition probabilities were obtained by averaging estimates from models 34, 35 and 36 (see Results and Table 2). 'EB' and 'FTB' denoted experienced and first-time breeders respectively.

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DISCUSSION

Correlative studies are not expected to correctly estimate an evolutionary link between two traits (Nichols & Kendall 1995, Viallefont et al. 1995). In absence of manipulation of the effort invested in reproduction, the cost of reproduction may indeed be masked by a quality-dependent breeding investment of individuals, where low quality individuals invest less with no apparent costs of reproduction (Reznick 1985, Van Noordwijk & Dejong 1986). Moreover, manipulative studies showed that Procellariiformes tend to transfer the unexpected costs of the current reproduction to their offspring without jeopardizing their future survival or future breeding attempt (Mauck & Grubb 1995, Mínguez 1998, Navarro & González-Solís 2007).

We did not find any indication of an overall cost of reproduction in relation to the current reproductive investment. In disagreement with the cost of reproduction hypothesis, we found that individuals that failed the current reproduction (i.e. invest less) had a lower future survival. Moreover, we did not find any evidence of a cost of reproduction on future breeding success. Individuals that survived had a higher probabilities of breeding successfully the following year likely due to a progressive selection of high-quality individuals (see also Forslund & Pärt 1995, Ratcliffe et al. 1998a, Mauck et al. 2004, Barbraud & Weimerskirch 2006). In fact, we found a positive relationship between fitness components in agreement with the selection hypothesis and other correlative studies on long-lived birds (Wooller et al. 1990, Cam & Monnat 2000, Barbraud & Weimerskirch 2006, O'Dwyer et al. 2006). Apart from the heterogeneity in individual quality, the lack of survival or fecundity costs associated with high reproductive investments can also be generated by favorable environmental conditions at breeding (Erikstad et al. 1998). Studies on long-lived mammals and seabirds showed that breeding probabilities and survival can be negatively influenced by poor environmental conditions (Hadley et al. 2007, Barbraud & Weimerskirch 2005). Thus, high levels of reproductive effort can generate a fitness cost detectable only when resources are limited (Tavecchia et al. 2005).

The influence of experience

Results from the first reproductive attempt were the only supporting the cost of reproduction hypothesis but again unrelated to the breeding effort. In fact first-time breeders, independently of their breeding success, survived less than experienced breeders. A cost of the first reproduction on survival and reproduction has also been reported for other long-lived species of both birds and mammals (Viallefont et al. 1995, Pyle et al. 1997, Cam & Monnat 2000, Tavecchia et al. 2001, Barbraud & Weimerskirch 2005, Tavecchia et al. 2005, Moyes et al. 2006, Nevoux et al. 2007), and it is probably related with the hormonal changes triggered by the first reproductive status (Harshman & Zera 2007). In addition, the lower survival of first-time breeders could reflect high proportions of low-quality individuals among this group, in accordance with the selection hypothesis (Wendeln & Becker 1999, Mauck et al. 2004, Barbraud & Weimerskirch 2006). Although survival probability in European storm petrels varied over the years, the survival difference between first-time and experienced breeders was constant and equal at the two study colonies, suggesting that stochastic environmental conditions may affect birds equally, independently of their breeding experience or success. Inexperienced breeders also showed an average lower current breeding success than experienced breeders, probably due to their lack of breeding experience (i.e. the breeding experience hypothesis, Ollason & Dunnet 1988, Bradley et al. 2000) and their intrinsic lower quality (Mauck et al. 2004, Barbraud & Weimerskirch 2006). However, first-time breeders are on average younger than experienced breeders and an experience-dependent cost of reproduction can be partially confounded by a positive effect of the age *per se* (Nur 1984, Forslund & Pärt 1995, Tavecchia et al. 2001). Moreover, Viallefont et al. (1995) showed that young first-time breeders of Snow goose *Anser caerulescens* were more likely to skip or to fail breeding the following season than older first-time breeders, and similar results have been reported for other long-lived birds (Weimerskirch 1990, Wooller et al. 1990, Barbraud & Weimerskirch 2005). Unfortunately, we were not able to fully estimate the relative effect of the age and the experience in the tradeoff pattern because for most of the birds only their experience was known, but a preliminary analysis of a small set of birds of known age does not support this hypothesis (results not shown).

Strikingly we found that first-time breeders that survived showed higher probabilities of breeding successfully in the following year than experienced breeders. Nevertheless, the model selection did not suggest a strong effect. This result may be the consequence of several non-exclusive factors. First, the presence of high proportions of old birds with, expected senescence in breeding performance, in the later group (Bradley & Wooller 2000); secondly, an intensive selection process of high quality individuals during the first reproduction (Forslund & Pärt 1995, Ratcliffe et al. 1998a, Mauck et al. 2004, Barbraud & Weimerskirch 2006); finally, the acquisition of breeding experience (Nur 1984, Ollason & Dunnet 1988, Bradley et al. 2000). Moreover the effect of the current breeding success on future breeding success was retained for first-time breeders, likely because those who bred unsuccessfully may have a small advantage in terms of future breeding success, in accordance with the cost of reproduction hypothesis (Stearns 1992, Roff 1992). Nevertheless, the model selection did not suggest a strong influence of the current breeding success.

In conclusion, results clearly supported the selection hypothesis, as unsuccessful and first-time breeders showed lower probabilities of survival than successful and experienced birds (Wooller et al. 1990, Wendeln & Becker 1999, Cam & Monnat 2000, Mauck et al. 2004, Barbraud & Weimerskirch 2006). The low survival and low initial breeding performance of first-time breeders found here suggested that the first reproduction represented a critical period, in line with other studies on birds (Viallefont et al. 1995, Pyle et al. 1997, Cam & Monnat 2000, Tavecchia et al. 2001, Barbraud & Weimerskirch 2005, Nevoux et al. 2007). Selective pressures during the first breeding event probably played an important role in the evolution of deferred breeding in long-lived species (Pyle et al. 1997). In fact, and with the exception of the first reproduction, we did not find any indication that breeding was costly for European storm petrels although we cannot exclude at present long-term cumulative costs of reproduction, as found in some long-lived mammals (Moyes et al. 2006). Future studies should also focus in handling among individuals heterogeneity. At present the incorporation of individual heterogeneity cannot be done using procedures based on likelihood. A possible way would be to obtained estimates based on Monte Carlo techniques (King et al. 2006) but the available methods at the moment are not flexible enough to handle complex models.

CAPÍTULO 4

EVIDENCE-BASED CULLING OF A FACULTATIVE PREDATOR: EFFICACY AND EFFICIENCY COMPONENTS

Evidence-based culling of a facultative predator: Efficacy and efficiency components

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ABSTRACT

Human activities have greatly modified predator-prey dynamics within seabird communities by favouring a rapid increase in density of large predatory gulls. To counteract such a subsidized growth, conservation agencies perform massive random culling programs, which generally fail to restore the original predator-prey relationship. We used long-term individual-based information to evaluate the effects of a selective culling of a top seabird predator, the yellow legged gull (*Larus michahellis*), on the predatory pressure, survival and reproductive success probabilities of a secondary prey, the vulnerable European storm petrel (*Hydrobates pelagicus*). The selective removal of only 16 gulls in 3 years led to a reduction of ca. 65% in the number of petrels killed, and to a relative increase in their survival and breeding success probabilities of 16% and 23%, respectively. Our results show that only a few specialised predators were responsible for the bulk of the impact on a secondary prey and that the removal of those specialised individuals was an effective and efficient way to improve prey demographic parameters.

Keywords: Breeding success, conservation, evidence-based management, storm petrel, survival, yellow legged gull.

INTRODUCTION

Seabird communities are characterized by networks of multiple interactions among species; many of these have been much altered in recent times by human induced changes in marine resources (Stenhouse & Montevecchi 1999, Solé and Montoya 2001, Votier et al. 2004b). These alterations have modified predator-prey dynamics within seabird communities owing to the negative effects of fisheries on fish stocks and by the increase of alternative food supplies, such as urban tips and fishery discards, which subsidize predators (Votier et al. 2004b, Furness et al. 2007). Gulls are the classic example of species affected by these deep and rapid changes; over the last century their populations have increased substantially (Oro et al. 1995, Thibault et al. 1996, Duhem et al. 2008) up to the point that large gulls are currently perceived as a pest by wildlife managers, for a large number of reasons, including their impact

on smaller and threatened syntopic species (Feare 1991, Vidal et al. 1998, Finney et al. 2003, though see Oro & Martínez-Abraín 2007). As a consequence, many conservation agencies have set up culling programs to control gull populations, which typically consist of systematic removal of large numbers of eggs, chicks or breeding adults (e.g. Blokpoel & Spaans, 1991). These programs are generally conducted at the local population level assuming that all individuals equally contribute to, or are equally responsible for, the conservation problem identified. This assumption is rarely supported and in most cases the systematic culling ends up being inefficient and unjustified (Oro & Martínez-Abraín 2007). On the contrary, Brooks & Lebreton (2001) showed that the optimal harvest strategy to limit the number of yellow legged gull (*Larus michahellis*) breeding pairs is to cull those individuals with the highest site/state-specific reproductive values. Likewise, the impact of predators may be only due to a few individuals specialised on a particular food item. Individual specialisation in diet is well documented in many animal taxa such as fish (e.g. Svanback & Persson, 2004), mammals (e.g. Estes et al. 2003) and birds (e.g. Spear 1993, Hario 1994, Guillemette & Brousseau 2001, Martínez-Abraín et al. 2003, Oro et al. 2005). In these cases, the optimal harvesting strategy would be to eliminate only specific individuals, regardless of their reproductive value, since a small number of specialist individuals may account for a significant proportion of particular prey consumed (Votier et al. 2004c). If effective, this strategy would minimize the cost of the control program and the impact of the predator leaving its total numbers almost untouched.

The most common facultative predator of seabird species in the Mediterranean basin is the yellow legged gull (Burger & Schreiber 2002). The species preys occasionally on eggs, chicks and adults of other seabirds, and is the target of systematic culling programs in many Mediterranean regions (Oro & Martínez-Abraín 2007). The Mediterranean storm petrel (*Hydrobates pelagicus melitensis*), a vulnerable seabird, is among the potential prey of yellow legged gulls (Mínguez 2004). Previous research showed that yellow legged gulls preyed upon both breeding and immature storm petrels and that this mortality was additive to other causes of mortality (Walmsley 1986, Zotier et al. 1992, Borg et al. 1995, Adam & Booth 2001, Oro et al. 2005). As gulls prey upon adult breeding storm petrels, the potential impact on

population viability is high since a whole set of life-history traits, such as low annual productivity, long reproductive cycles, delayed reproductive maturity and low adult mortality, make petrels particularly vulnerable to factors affecting adult survival (Warham 1990, Saether & Bakke 2000). Adult storm petrels are an occasional component of the yellow legged gull diet, and it may well be that only a few gulls have learnt how to exploit this secondary food resource (Oro et al. 2005). In this case, a systematic culling is likely to be an inefficient and improper measure of control.

Here we simultaneously evaluate the effects of a selective culling of a top seabird predator on the survival, reproductive success and predatory pressure of a secondary prey. We report an experimental study on the evidence provided by an *ad hoc* research program on a western Mediterranean island, holding both a storm petrel and a yellow legged gull colony, to encourage evidenced-based conservation (Pullin et al. 2004). The burrowing nesting habits of petrels make it difficult to obtain reliable estimates of population abundance, and an insight into its population dynamics can only be obtained by the estimate of demographic parameters from individual-based data (Oro et al. 2004b). We tested the hypothesis that selective culling triggered a decrease in predation and, in turn, an increase in petrel survival and/or reproduction parameters. Using detailed information on marked individuals we then estimated the impact of predation on these parameters to experimentally evaluate the demographic consequence of gull removal.

METHODS

Study area and predatory-prey dynamics

The study was conducted from 1993-2007 at Benidorm Island (6.5ha; 38°30'N, 0°08'E), a Special Protection Area for the conservation of the European storm petrel species in the western Mediterranean coast of Spain. Gull numbers on the island have recently increased and evidence of predation on storm petrels (see below) has encouraged managers to control the yellow legged gull population.

The yellow legged gull is a large long-lived gull (average body mass, 800-1500 g, Cramp & Simmons 1977). Eggs, usually three, are laid from mid March to early May and incubated for 27-31 days and the young birds fledge after 35-40 days. Nests are typically built on the ground or on cliff ledges. Gull territories are defended by both sexes and in stable habitats, e.g. rocky islands as opposed to sandy islands, gulls often show a high degree of fidelity to colony sites (Mac Nicholl 1975, Burger & Lesser 1980). An average of 535 pairs of yellow legged gulls (median = 515, range = 300-750) have bred annually at Benidorm during the last 10 years, with a mean population growth rate of 6% during 1993-2007 (95%CI = 1.04-1.09) (see also Oro & Martínez-Abraín 2007). Gulls nest mostly on open ground but a few pairs breed in close proximity to the two major petrel colonies.

The European storm petrels are small (average body mass, 28 g, Warham 1990) and long-lived vulnerable seabirds. They are single egg layers with an extended breeding period (incubation lasts about 40 days and chick rearing about 63-70 days). Earliest clutches are laid in the second half of April and the last eggs are laid in the first week of July (Mínguez 1994). Most fledglings leave colonies in August (Mínguez 1994). At their breeding colonies, adult European storm petrels return to land only during the hours of darkness (Mínguez 1996). Despite the prevalence of nocturnal activity, petrel eyes show no obvious adaptations for life in the night (Warham 1988). In fact, storm petrels use odour signals to find their nest (De León et al. 2003). It is likely that adult storm petrels are captured by gulls at night when they land before entering the protection of their nesting sites. In addition, gulls can take young petrels, which venture to the entrance of their burrows to exercise their wings (Sultana & Gauci 1970). The breeding population of storm petrels at Benidorm Island has been estimated at more than 400 pairs (Mínguez 1994). Petrels breed all around the island at low densities but concentrate at high densities in two natural caves, where more than 300 pairs breed. We focused on data from the largest breeding colony (>200 breeding pairs), where most predation events were recorded (Oro et al. 2005). Since 1993 breeding storm petrels were captured and marked in their nests with stainless steel bands, with a unique alphanumeric code. Breeding birds were captured only once during the breeding season to minimize disturbance, but nests were inspected at

least four times during the whole breeding period to record breeding success (Mínguez 1994, Tavecchia et al. 2008).

<p style="text-align: center;">*Evidence of gull predation and design of the selective culling*</p>

Evidence of petrel predation by gulls on the study site has been known for a long time but only since the gull population increased have there been attempts to quantify its impact (Díez & Martínez-Abraín 1989, Massa & Sultana 1993, Mínguez 1994). Petrel predation was assessed by the inspection of indigestible food items in pellets collected opportunistically near gull nests or around the petrel colony during 1993-2001. Although the whole island is inspected by researchers and wardens regularly for different monitoring tasks, fewer than 10 pellets containing petrel remains per year were found far from petrel colonies. From 2002 to 2007, we standardized pellet collection with a systematic search at the vicinity of petrel colonies (see details in Oro et al. 2005). The minimum number of petrels killed by gulls was estimated as half the number of pellets containing petrel remains found because gulls produce two pellets for every storm petrel eaten (Oro et al. 2005). We identified those pairs that predated upon storm petrels by searching for pellets from April to June within three meters around gull nests, an area that we arbitrary identified as a gull territory (Oro et al. 2005). About 50 territories of gulls were inspected annually for evidence of predation to identity 'specialist' pairs, i.e. with more than one pellet with petrel remains found in their territories (Oro et al. 2005). The impact on marked birds was quantified by the number of rings of breeding petrels recovered in gull pellets. The impact of gull predation before and after the culling program was compared using a χ^2 test.

The Environmental Monitoring Service of Benidorm Island (Natural Park Serra Gelada -Generalitat Valenciana) and personnel from the Endangered Species Research Team (Generalitat Valenciana) carried out an egg-pricking program from 2001 to 2006 with no apparent effects on gull numbers (Martínez-Abraín et al. 2004) or on the number of pellets containing petrels' remains (this study). A second measure of control was to selectively remove those gulls that bred near petrel colonies thought to be responsible for most predation events (Borg et al. 1995,

Adam & Booth 2001, Oro et al. 2005). From 2004 to 2005 a total of 6 gulls breeding in territories previously identified as belonging to 'specialist' pairs (i.e. 1 pair that bred inside the petrel's cave and 2 individuals belonging to 2 different territories located outside the cave in 2004, plus 2 individuals that bred in two territories located outside the cave in 2005) were captured with nest traps placed on the nests. In 2006, 10 additional individuals (i.e. 3 pairs plus 4 individuals from different territories) were trapped on nests located at the edge of the petrel colony as a precautionary measure. In all cases nests were deserted. All individuals were killed by an authorised wildlife agent through the injection of an excess sedative in the jugular vein.

Demographic parameters and culling efficacy

Adult survival probability of petrels was estimated from 1858 observations of 675 breeding adults marked from 1993 to 2007. These data were analyzed using capture–recapture models, which estimate survival and detection probabilities simultaneously (see details in Lebreton et al. 1992, Amstrup et al. 2005). The analysis compared models in which survival and recapture probabilities depended on a different combination of the factors considered (see below). Models were selected using Akaike's Information Criterion (AIC) and Akaike weights (w_j, for each model j) were calculated as an index of the strength of evidence of each model (Burnham & Anderson 2002). Model selection began by assessing the goodness of fit of a general model in which all parameters were time-dependent, i.e. the Cormack-Jolly-Seber model (Lebreton et al. 1992), by contingency tables, together with the Chi-square statistic, using program U-CARE 2.2.2 (Choquet et al. 2005). Model deviances and AIC values were calculated using program M-SURGE (Choquet et al. 2004).

Average breeding success was modelled as a binary variable (1=successful, 0=unsuccessful) using generalized linear mixed models with a logit-link function and binomial error distribution (McCulloch & Searle 2001). Analyses were conducted with the R statistical package (www.R-project.org/) using the glmmML function in which 'year' (15 levels) was considered a fixed term and the nest identity treated as a random term to prevent pseudoreplication.

Together with identifying the most parsimonious model to describe the parameter considered, our analysis also aimed to test for a difference in survival and breeding success before and after the selective culling. The comparison was done using a Likelihood Ratio Test (LRT, Lebreton et al. 1992) between a model including a single parameter for 1993-2007 with one assuming two parameters, one for the period before the culling (1993-2003) and a second for the period after (2004-2007, denoted 'culling' in model notation). The test was based on the change of deviance between the two nested models.

RESULTS

Evidence of gull predation and selective culling

The number of pellets containing petrel remains found during April and May 2004, when the selective culling began, was similar to the one in previous years. However, after the removal in early June of a single gull the evidence of predation decreased drastically (see Fig 1).This last individual was the male from a pair breeding inside the cave where the petrel colony is located, so their breeding territory was within the petrel colony. In 2005 and 2006 the number of pellets containing petrel remains remained low with the exception of August 2006, when a group of juvenile gulls spent several nights inside the cave that hosts the colony (direct observation, Fig 1). A few of the gull territories from which adult gulls were removed were reoccupied during 2007 when culling was stopped. There was no apparent increase in predation rates following this colonisation (Fig 1). Overall, removal of only 6 specialized gull and 10 additional individuals nesting in the proximity of the cave led to a mean reduction of 65% (95%CI= 57-72) in the number of petrels found in gull pellets (χ^2 =157.14, d.f.=1, P<0.001) (Table 1, Fig 1). After 2004 we also found a mean reduction of 89% (95%CI= 85-94) in the number of metal rings of breeding petrels inside the pellets compared with the period 2002-2003 (χ^2 =18.38, d.f.=1, P<0.001), when field protocol to collect pellets was the same but in absence of culling (Table 1).
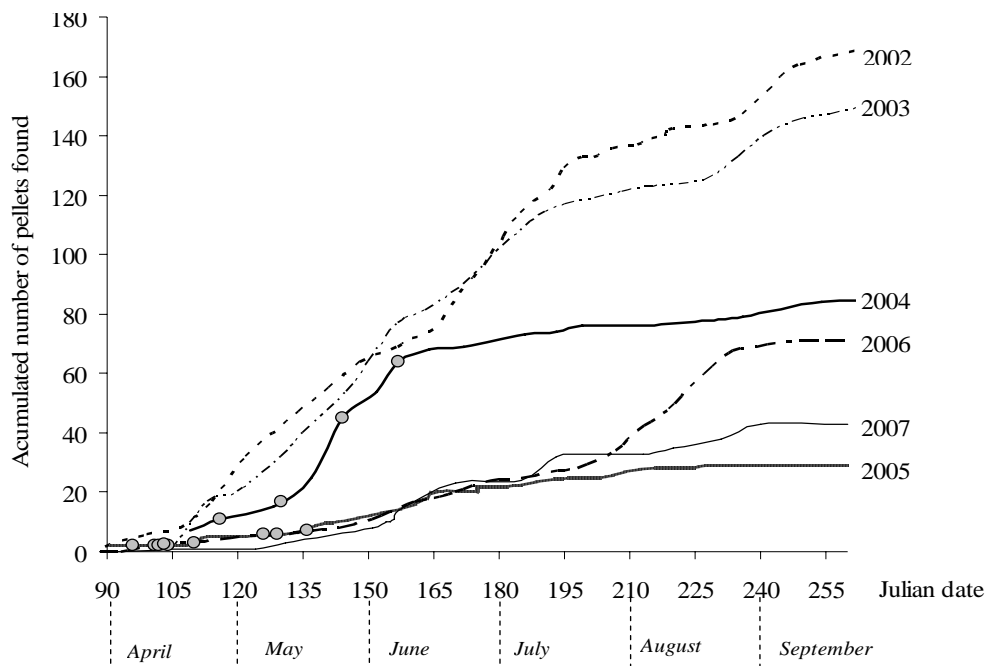
FIGURE 1. Acumulated daily number of pellets containing remains of storm petrels found at Benidorm Island, western Mediterranean, from 2002 to 2006. Dots indicate the days of gull culling

TABLE 1. Evidence of predation of European storm petrels by yellow legged-gulls during years of systematic collection of gull pellets containing petrel remains (2002-2007). The number of petrels killed was estimated as half the number of pellets including rests of petrels (Oro et al. 2005). Selective culling was conducted from 2004 to 2006 and egg-pricking from 2001 to 2006.

Year	2002	2003	2004	2005	2006	2007
Yellow legged gull breeding pairs	432	515	508	610	750	687
Selective culling	No	No	Yes	Yes	Yes	No
Egg-pricking	Yes	Yes	Yes	Yes	Yes	No
No. of pellets with petrel remains found	171	150	84	29	71	43
Estimated no. of petrels killed	86	75	42	15	36	22

Demographic parameters and culling efficacy

The overall test of goodness of fit of the CJS model was statistically significant (χ^2 =96.18, d.f.=46, P<0.001) because newly marked birds had a lower survival than birds already marked (χ^2 =48.12, d.f.=13, P<0.001), and the current recapture

probability depended on the past recapture probability (χ^2 =27.91, d.f.=12, P=0.006). As a consequence we considered a model with two age-classes for survival parameters (a model including a 'transient' effect as detailed in Pradel et al. 1997) and we used a variance inflator factor, $\hat{c}$-hat, calculated as the ratio of the global chi-square statistic on its degrees of freedom, to correct for the residual lack of fit ($\hat{c}$-hat=1.46; Lebreton et al. 1992). In agreement with a previous study (Tavecchia et al. 2008) we found a high recapture probability (average value: 0.79, 95%CI=0.75-0.81) that varied over the study period (model 3, Table 2, Fig 2). The retained model assumed a parallel variation on survival probabilities between newly and already marked birds over the study period (model 3, Table 2). Likelihood ratio tests showed that the culling program had a statistically significant effect on survival probabilities of resident birds (model 10 vs. model 4, Table 2, χ^2 =21.56, d.f.=1, P<0.001) but we did not find statistically significant differences in the survival of newly marked birds (model 11 vs. model 4, Table 2, χ^2 =2.07, d.f.=1, P=0.151). Before the removal of specialists gulls, resident storm petrels showed a mean adult survival probability of 0.75 (95%CI=0.71-0.78). This value increased to 0.89 (95%CI=0.82-0.94) after the selective culling of gulls (model 7, Table 2, Fig 3a). From these values we can estimate the mortality caused by yellow legged gull predation at 16%.

TABLE 2. Modelling recapture 'p' and survival 'Φ' probability of adult European storm petrels. np: number of estimable parameters; Dev: relative deviance; QAIC: Akaike information criterion corrected by $\hat{c}$-hat; Δ_i: the QAIC difference between the current model and the one with the lowest QAIC value; w_i: Akaike's weight. Model notation: 't'=time effect, 'cull'= effect of culling (2 parameters, one for the period 1993-2001 and one for 2002-2007, respectively), '+'=parallel variation between survival of newly and already marked birds, '.'= constant (i.e. no effects considered). The model retained is in bold.

Model	p	$\Phi_{transients}$	$\Phi_{residents}$	np	Dev	QAIC	Δ_i	w_i
1	t	t	t	40	2953.27	2108.34	9.83	0.01
2	.	t	t	28	3009.11	2122.70	24.19	0
3	**t**	**t+**	**t+**	**29**	**2790.99**	**2098.51**	**0**	**0.83**
4	t	.	.	16	3047.94	2125.36	26.85	0
5	t	t	.	29	2990.96	2112.23	13.72	0
6	t	.	t	28	3007.42	2121.54	23.02	0
7	t	t	cull	30	2972.96	2101.87	3.36	0.16
8	t	cull	cull	18	3021.55	2111.24	12.73	0
9	t	cull	t	29	3000.47	2118.77	20.25	0
10	t	.	cull	17	3026.38	2112.56	14.04	0
11	t	cull	.	17	3045.87	2125.94	27.43	0
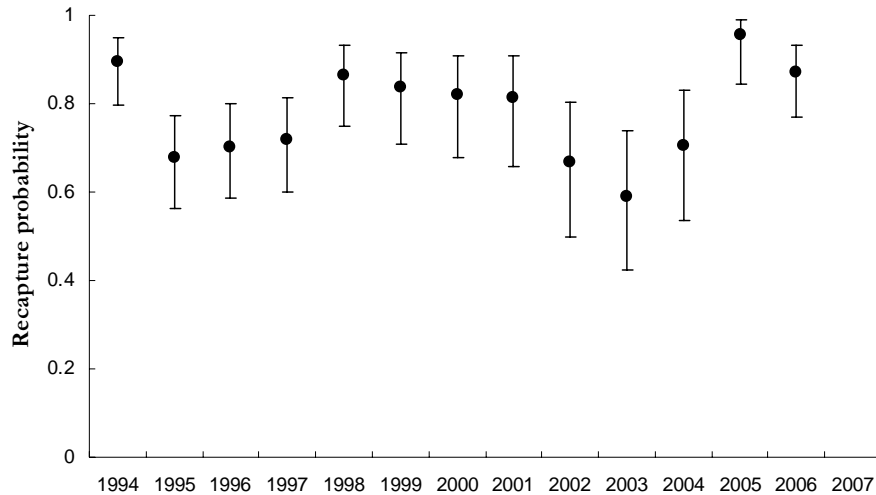
FIGURE 2. Annual estimates (± 95%CI) of storm petrel's recapture probabilities from model 3 (Table 2). The last recapture probability is not shown because it is not separately identifiable.

For the breeding success, the most parsimonious model (model 1, Table 3) included an effect of time (Table 3, Fig 3b). As for survival probabilities, likelihood ratio tests showed that the culling program had a statistically significant effect on breeding success (χ^2 =39.00, d.f.=1, P<0.001) (Table 3) that increased from 0.50 (95%CI=0.48-0.53) before 2004 to 0.66 (95%CI=0.62-0.70) after the removal of specialist gulls. These values indicate that predation by gulls reduced the average breeding success probabilities by 23%.
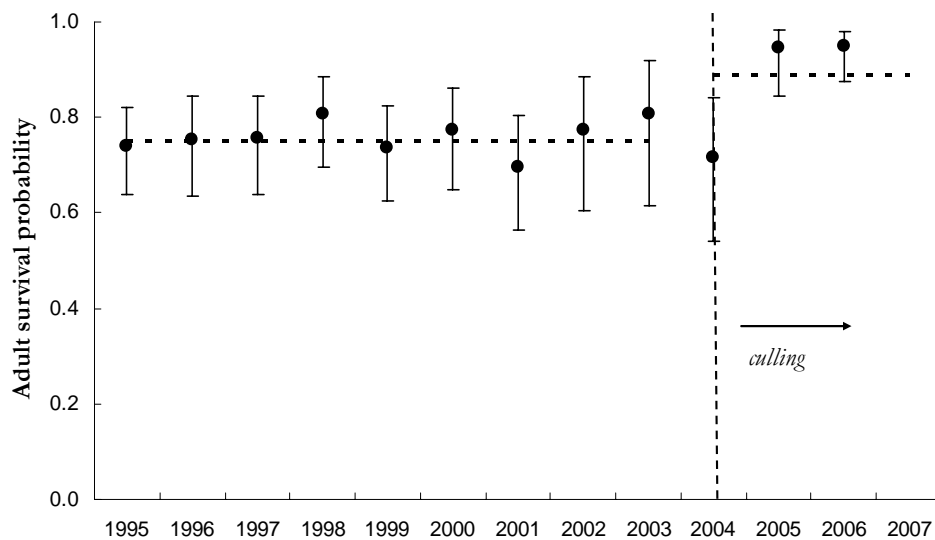
FIGURE 3a). Demographic parameters of the European storm petrel before and after the selective culling of specialist gulls. Annual estimates (± 95%CI) of survival probabilities of resident birds from model 3 (Table 2). Note that the last survival probability is not shown because it is not separately identifiable from recapture probability.

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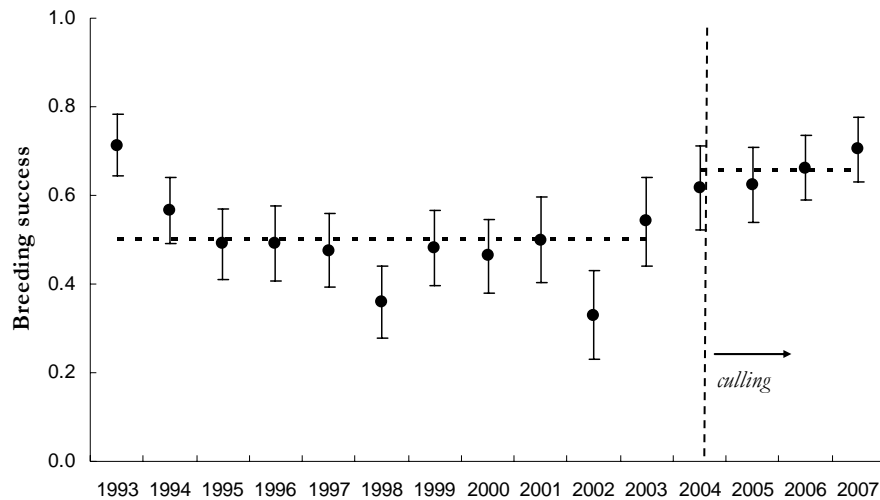
FIGURE 3b). Demographic parameters of the European storm petrel before and after the selective culling of specialist gulls. Annual breeding success (Model 1; Table 3). Broken horizontal lines indicate average estimates before and after the culling program began, respectively (Model 7, Table 2 for survival and Model 2, Table 3 for breeding success).

TABLE 3. Breeding success of European storm petrels analysed through Generalized Linear mixed modelling; np: number of parameters; Dev: relative deviance; AIC: Akaike information criterion; Δ_i: the AIC difference between the current and lowest AIC model; w_i: Akaike's weight. Model notation:'t'=yearly variation, 'cull'= effect of culling (2 parameters for the period 1993-2001 and 2002-2007, respectively), '.'= constant (i.e. no effects considered). The model retained is in bold.

Model	Effects	np	Dev	AIC	ΔAIC	w_i
1	**t**	**15**	**2587**	**2619**	**0**	**1**
2	cull	2	2655	2661	42	0
3	.	1	2694	2698	79	0

DISCUSSION

Our experimental results showed that i) predation by gulls affected negatively both adult annual survival probability and breeding success of syntopic petrels, and ii) after removing specialist gulls, adult survival probabilities and breeding success of storm petrels greatly and rapidly increased (16% and 23%, respectively). Although 16 gulls were removed during the study period, we believe that the specialist gull pair removed in 2004 that bred within the major petrel colony was responsible for most

predation events. Indeed, predation levels in 2004 greatly decreased after removal of the male of that pair (early June 2004, Fig 1). Our results are in agreements with those of Spear (1993) who found that specialist gulls were mainly territorial males and represented a tiny proportion of the population (ca. 1%). Previous studies have documented the efficacy of selective culling of specialist gulls to enhance the breeding success of their secondary prey (Hario 1994, Guillemette & Brousseau 2001). Our results are consistent with those findings but also show the efficacy of a selective culling to enhance prey survival probabilities. This result was relevant since population growth rate of long lived species is especially sensitive to changes in adult survival (Saether & Bakke, 2000). Before the removal of specialist gulls, petrel adult survival estimated in our study site was lower than estimates from predator-free colonies such as those in Biarritz (France) (0.90-0.95; Hemery 1980) or Marettimo (Italy) (0.88, CI95%=0.85-0.91; Sanz-Aguilar et al. 2009b). Specialist adult gulls can be individually identified and removed at the beginning of the petrel breeding period due to their territorial habits (i.e. remains of their main prey can be easily found around their nests). Unfortunately, culling of territorial specialist gulls cannot alleviate predation by juveniles. Presence of juvenile gulls inside caves where petrels breed is common from July to September (Mínguez & Oro 2003). Nevertheless, at Benidorm Island predation by juvenile gulls seems to have a strong stochastic component. For example, predation by juvenile gulls was recorded in 2006 but not in 2004, 2005 or 2007. Identification of specialist juveniles is nearly impossible even by direct observation of predation events. Despite this, it is likely that juvenile gulls prey upon fledgling petrels rather than adults, so have a much reduced impact on petrels' population growth rate (Saether & Bakke 2000). The success of the management actions implemented at Benidorm Island encourages management decision-making based on previous evidence. Studies investigating the effectiveness of interventions are highly relevant to practitioners but few studies actively test or review conservation actions (Fazey et al. 2005, Armstrong & Seddon 2008). During the last year of study no gulls were removed and predation rates continued at low levels, suggesting that most specialist gulls were removed in previous years. Although gulls from reoccupied territories inside the cave holding the petrel colony did not specialise as petrel predators in 2007, monitoring and management actions should be implemented on an annual basis, since gulls can readily occupy such a foraging niche

(Spear 1993, Guillemette & Brousseau 2001). Moreover, new fishing and environmental policies, including reductions of trawling discards and closure of landfills, will reduce important foraging resources for gull populations (Oro et al. 2006). Under this scenario it is expected that facultative predators increase predation rates on smaller syntopic species (Stenhouse & Montevecchi 1999, Votier et al. 2004b). Intensive control measures are often very onerous (Table 4) and necessitate heavy manpower and resources. Egg-pricking is an efficient method to reduce gull nesting success (Smith & Carlile 1993), nevertheless adults remain alive at colonies and may continue preying upon vulnerable species. Culling of breeding adults can be carried out by placing poisoned baits in gull nests (Bosch et al. 2000) or with nest traps (this study). The first technique requires one visit to place the first bait in each nest, a new visit to remove the dead gulls and to place new baits, and a final visit to remove both newly killed gulls and any remaining bait (Bosch et al. 2000). Several hours are allowed to elapse between consecutive visits, allowing narcosis. Moreover, it is necessary to transport culled birds to land in order to remove them by incineration and search those that died at sea from a boat to prevent secondary poisoning (Bosch et al. 2000). Placing nest traps to capture gulls is much more time consuming than placing poisoned baits and it would be impractical for a massive culling program (Table 4). Massive culling programs can be successful to reduce gull numbers or reduce the effect of gull predation (Bosch et al. 2000, Finney et al. 2003, Paracuellos et al. 2006) only at small temporal and spatial scales (Skira & Wapstra 1990, Bosch 1996, Harris & Wanless 1997, Vidal et al. 1998, Oro & Martínez-Abraín 2007). In addition, massive random culling programs have the indirect effect of enhancing dispersal (Coulson 1991, Bosch et al. 2000), so that the reduction in gull numbers in a local population may be rapidly compensated by an increase of recruitment due to density-dependent regulation (Brooks & Lebreton 2001). Moreover, culling on adult birds has the potential to increase young survival because of decreased competition for food resources that remain at a static level (Coulson et al. 1992). Thus, to substantially reduce gull numbers at a metapopulation level it may be necessary to kill a large number of individuals for a long period, which is an expensive and polemic solution (Bosch et al. 2000).

TABLE 4. Estimates of time costs (hours) for specific (10 individuals) and massive (800 individuals) gull culling programs using nest traps to capture gulls or by narcotizing gulls whit poisoned baits. We considered 100% of effectiveness (i.e. both members of the pair die). We considered for each strategy: Preparing baits= 2min/bait; Setting traps=15min/trap; Setting baits=3min/bail; Kill gulls=10min/gull; Recollect dead gulls=10min/gull. Note that for the sake of simplicity costs for people, for transport of dead gulls or for the search of nests or gulls dead at sea were not considered.

Costs (hours)	Nest traps		Poisoned baits	
	Specific	Massive	Specific	Massive
Preparing baits	0	0	0.33	26.4
Search 'objective' nests	24	0	24	0
Setting traps or baits	2.5	200	0.5	40
Kill gulls	1.66	133	0	0
Recollect dead gulls	1.66	133	1.66	133
Total	**30**	**467**	**26**	**200**

The implementation of specific culling programs is both time and resource consuming but such costs are negligible compared to the traditional solution of a systematic massive culling of individuals, not to mention social or ethical costs (Oro & Martínez-Abraín 2007) as well as unforeseen and unwanted side effects (Martínez-Abraín et al. 2004). This is especially true when most predation is caused by specialist gulls, and consequently massive random gull culling may not be a practical solution (Hario 1994). A massive culling program performed in Alborán Island, Western Mediterranean, Spain, from 2000 to 2006, successfully removed around 28.6% (range: 16-45%) of pairs breeding in the island annually (Mariano Paracuellos, *com. pers.*). Similar results were obtained through a systematic massive culling at Medes Islands, where between 21 and 29% of the breeding adults were killed annually (Bosch et al. 2000). Consequently, the presence of specialist predators may be omitted from a general cull just by chance. Specialist bird predators defend breeding and feeding territories, retain their feeding habit and feeding territory across years (Votier et al. 2004a). Removing only specialized individuals is a much more efficient solution to protect species of conservation-concern when threatened by excessive predation owing to human subsidizing of predators (e.g. increased predator density by increased availability of food resources) (Shapira et al. 2008, Gompper & Vanak 2008). Our study clearly illustrates the great potential of evidence-based wildlife management (Pullin et al. 2004) in terms of resource optimization and successful achievement of desired conservation goals.

DISCUSIÓN GENERAL

Ana Sanz Aguilar

En esta tesis se han integrado enfoques metodológicos, ecológicos y evolutivos destinados al estudio y conservación del paíño europeo. Se han comparado diferentes métodos de monitoreo de poblaciones; se ha analizado la variabilidad espacio-temporal de los parámetros poblacionales; se han estudiado los patrones de reclutamiento de la especie; se ha indagado en en los compromisos evolutivos de los rasgos de historias de vida; y finalmente se ha evaluado la eficacia de una actuación de conservación, encaminada a disminuir la mortalidad de los individuos, llevada a cabo en base a evidencias previas.

MÉTODOS DE MONITOREO Y ESTIMACIÓN DE PARÁMETROS POBLACIONALES

La presente memoria ha mostrado cómo los métodos de monitoreo mediante captura de individuos de especies nocturnas con hábitos de cría hipogeos, como el paíño, influencian en la precisión de las estimas de los parámetros poblacionales de interés. El uso de redes en el entorno de las colonias de cría, especialmente en combinación con reclamos sonoros, permitió capturar una gran cantidad de individuos pero el porcentaje de individuos recapturados en ocasiones sucesivas fue muy bajo (Capítulo 1). En los nidos tan sólo se capturan individuos reproductores o pollos mientras que en redes también se capturan individuos prospectores no-reproductores que no pueden ser fácilmente diferenciados de la fracción reproductora (Furness & Baillie 1981).

Generalmente, uno de los principales objetivos de los estudios de captura-recaptura de aves es estimar el tamaño de la población. Ninguna de las metodologías de captura de paíno europeo habitualmente utilizadas permitieron obtener estimas robustas de tamaño poblacional dado el incumplimiento de las asunciones del modelo, es decir, la existencia de una heterogeneidad inter-individual en la supervivencia (presencia de individuos transeúntes) y en la recaptura (dependencia de la trampa), y a que el monitoreo en nidos da acceso a tan sólo una fracción de las poblaciones reproductoras (Capítulo 1). Durante el transcurso de esta tesis se intentó estimar el tamaño de la población reproductora de paíño en las dos colonias de la isla de

Benidorm a través de modelos de captura-recaptura diseñados para poblaciones cerradas (resultados no mostrados). La idea consistía en la captura y marcaje de pollos en sus nidos, la posterior recaptura de los mismos en redes en la entrada de ambas cuevas y la corrección de las estimas en función del éxito reproductor de las colonias. A pesar de que se anillaron más de 100 pollos en el interior de las colonias, no se recapturó ninguno con las redes de forma que no se pudo obtener ninguna estima de tamaño poblacional.

Tanto mediante métodos de captura en red como en nido, se obtuvieron estimas de supervivencia adulta de las aves residentes y de proporción de transeúntes que parecen razonables en base a la biología (ave longeva) y variabilidad de las presiones de depredación por gaviota patiamarilla de las diferentes zonas de estudio (Capítulo 1). Sería interesante poder evaluar las diferentes metodologías de captura en un mismo intervalo temporal y en la misma colonia para poder comparar las estimas obtenidas mediante cada uno de los métodos de captura sin tener que tener en cuenta la variabilidad espacio-temporal que potencialmente puede existir en los parámetros demográficos (ver Capítulo 2). Sin embargo, no disponemos de este tipo de datos y su recolección supondría aumentar el nivel de molestias ocasionadas por los investigadores sobre las aves reproductoras. Al tratarse de un ave "Vulnerable" y relativamente sensible a los efectos de la manipulación (Blackmer et al. 2004), dicho estudio no estaría suficientemente justificado.

A la hora de planificar un estudio encaminado a la estimación de parámetros poblacionales a través de técnicas de captura-marcaje-recaptura, es imprescindible determinar a priori cuáles van a ser los parámetros de interés y la precisión que se desea obtener en sus estimas. Las estimas obtenidas únicamente van a ser fiables si se respetan las asunciones implícitas de los distintos modelos (Link 2003). Los análisis de potencia pueden ser muy efectivos para calcular el número de individuos que es necesario marcar si que quieren obtener medidas de variabilidad temporal o entre grupos. Es necesario tener en cuenta los rasgos de vida y características comportamentales de la especie. Más importante que la cantidad de datos recogida (como el número de individuos marcados) es su calidad (recapturas frecuentes y regulares). La utilización de diferentes técnicas de captura y la heterogeneidad en el

esfuerzo invertido en el monitoreo en un área de estudio dificulta la modelización de los datos y/o la interpretación de las estimas obtenidas.

El seguimiento individual del paíño europeo mediante su captura en nidos presenta la ventaja, con respecto al seguimiento mediante captura en redes, de poder estimar, además de la supervivencia, parámetros como el éxito reproductor (Capítulos 2, 3 y 4) o el reclutamiento (Capítulo 2). Sin embargo, es habitual que los nidos de esta especie se encuentren en zonas inaccesibles, por lo que mediante un protocolo de captura de los individuos en redes destinado a maximizar las recapturas se puede estimar con precisión el parámetro con mayor influencia en la viabilidad de sus poblaciones, es decir, la supervivencia adulta (Capítulo 2).

PARÁMETROS DEMOGRÁFICOS DE LAS POBLACIONES DE PAÍÑO EUROPEO

Los individuos transeúntes

Una característica común a todas las colonias de paíño estudiadas fue la presencia de individuos "transeúntes", aves que desaparecieron después del marcaje (Capítulos 1, 2, 3 y 4). Sin embargo, la proporción de transeúntes entre la población residente dependió de la colonia y el método de captura (Capítulo 1). Mediante el uso de redes para la captura de individuos se incrementaba el número de aves "transeúntes" capturadas. Este hecho podría deberse a la captura de una gran proporción de aves prospectoras (no reproductoras). La presencia de individuos transeúntes también se detectó entre la población reproductora. Este fenómeno podría responder a un coste de la primera reproducción en la supervivencia (Capítulo 3), aunque no se puede descartar una mayor dispersión permanente de los individuos tras la primera manipulación. Hasta el momento no se tienen datos que puedan corroborar esta hipótesis ya que tan sólo se posee evidencia de cambio de colonia reproductora de cinco individuos entre ambas cuevas de Benidorm en 16 años de estudio y ninguno de los individuos reproductores capturados en sus nidos ha sido posteriormente recapturado mediante el uso redes en ninguna otra colonia.

Durante los años 2005 y 2006 se recogieron numerosas muestras de sangre de paíños en las colonias de Benidorm con el objetivo de encontrar un discriminante

morfológico del sexo. Debido al pequeño tamaño de esta especie, y el consiguiente error de medida relativo, no se consiguió dicho discriminante. Sin embargo los datos de sexado genético han permitido modelizar la supervivencia en el periodo 2005-2008 en función del sexo (resultados no mostrados). Un reciente análisis preliminar apunta a que tan sólo se aprecia un efecto transeunte entre las hembras, lo que podría indicar un coste de la primera reproducción en la supervivencia y/o una mayor dispersión de hembras. Se trata de un punto interesante a explorar en profundidad en un futuro.

El reclutamiento

Los procesos de reclutamiento de nuevos individuos en las colonias de cría son particularmente difíciles de estudiar en especies con características similares a las del paíño, es decir, primera reproducción tardía, movimientos a grandes escalas durante el periodo post-reproductivo y dificultad de monitoreo. El porcentaje de reclutas (i.e. individuos marcados como pollos y recapturados como reproductores en el periodo de estudio) fue bajo, de un 6-7% (Capítulo 2). Este hecho pone de manifiesto la necesidad de marcar una gran cantidad de pollos durante largos periodos de tiempo para poder obtener estimas precisas de reclutamiento y parámetros demográficos por clases de edad.

Entre los reclutas capturados, se encontró un sesgo en su distribución de sexos (Capítulo 2). El número de machos fue mayor, lo que podría responder a la razón natal de sexos observada, que estaba sesgada hacia los machos, sin excluir la posiblilidad de que exista una mayor dispersión pre-reproductora en hembras.

Se observó una tendencia filopátrica en el reclutamiento a pequeña escala espacial (Capítulo 2). Las aves que reclutaron en su colonia de nacimiento mostraron preferencia hacia el mismo sector de la cueva donde nacieron (Lo Valvo & Massa 2000). Entre ambas cuevas de la isla de Benidorm el 95% de los reclutas comenzaron su reproducción en su colonia de origen. Estos hechos tan sólo revelan patrones a pequeña escala y no implican que puedan existir movimientos dispersivos a otras colonias a escalas geográficas mayores. De hecho, tan sólo se recapturó un pequeño porcentaje de los individuos marcados como pollos. Como se ha mencionado

anteriormente, sería necesario anillar gran cantidad de pollos y monitorizar diferentes colonias para estudiar los patrones espaciales de reclutamiento en la especie. Los estudios genéticos también podrían contribuir a mejorar el conocimiento del grado de conectividad entre las diferentes colonias de la especie.

Se observaron diferencias intercoloniales en la edad de la primera reproducción y en las curvas de reclutamiento en función de la edad (Capítulo 2). En Marettimo, algunos paíños empezaron a criar con un año y el grueso de los reclutas fue incorporándose progresivamente a la fracción reproductora, alcanzando el pleno reclutamiento a los 5 años. En las dos colonias de Benidorm la edad observada de la primera reproducción fue más tardía, 3 años, pero el pleno reclutamiento se dió a edades más tempranas: 3 y 4 años en cada una de las dos colonias. No pudimos encontrar una explicación simple para estas diferencias observadas tanto a pequeña como a gran escala espacial. Tal vez estén jugando un papel en la modulación de la edad de reclutamiento la presión por depredación, las condiciones del medio o la disponibilidad de lugares aptos para la cría. Sería necesario continuar recopilando información para elucidar cuáles son los factores que están influenciando el reclutamiento en esta especie.

La supervivencia

El parámetro sin duda más importante para la persistencia de las poblaciones de paíño, como de todas las especies longevas, es la supervivencia adulta. Se observó que la supervivencia local aumentaba con la edad en las tres colonias en las que se disponía de datos para evaluar este efecto (Capítulo 2). Es importante aclarar que las estimas obtenidas se refieren a supervivencia local, ya que el modelo considera como "muertos" a aquellos individuos que potencialmente podrían haber reclutado fuera de las áreas de estudio. Una limitación de este análisis fue la escasez de datos de las primeras clases de edad, que impidió modelizar independientemente la supervivencia de las primeras clases de edad (1 y 2 años en Marettimo, y hasta los 3 años en Benidorm). Como las primeras clases de edad habitualmente no son observables en esta especie (son prospectores no-reproductores), obtener estimas de su supervivencia es especialmente complicado. Para analizar si los individuos de 3 años (edad de la primera reproducción en Benidorm) presentaban probabilidades de

supervivencia menores a la de individuos que comenzaron su reproducción a edades más tardías se realizó un análisis (resultados no mostrados) en el que los individuos fueron agrupados en relación a su edad de la primera reproducción (3 años, 4 ó mas). Dicho análisis no reveló diferencias entre grupos, aunque el tamaño muestral era pequeño, lo que parece sugerir que el coste de la primera reproducción en la supervivencia observado podría únicamente depender de la experiencia (Capítulo 3) y no de la edad. Debido al reducido número de individuos de edad conocida en las bases de datos no se ha podido profundizar más en la influencia de la edad en la supervivencia, por ejemplo si a edades avanzadas se observa una disminución de la supervivencia por fenómenos de senescencia. Sin embargo, el número de observaciones aumenta rápidamente cada año de estudio, con lo que en un futuro sería interesante evaluar de forma más precisa la influencia de la edad en los parámetros demográficos.

La supervivencia adulta del paíño varió tanto a escala espacial como temporal (Capítulos 1, 2, 3 y 4). Los valores medios más bajos se estimaron para las colonias de la isla de Benidorm, entorno a un 70%. Estos valores tan bajos se debieron a la intensa depredación que sufría la especie con anterioridad a la puesta en marcha de un programa de manejo de las parejas especialistas de gaviota patiamarilla (Capítulo 4). En las colonias donde aparentemente no existe una gran presión depredadora por parte de las gaviotas (Marettimo, Hormigas) las estimas de supervivencia adulta media se situaron entorno al 90% (Capítulos 1 y 2), valor muy similar al estimado en Benidorm tras la eliminación selectiva de depredadores (Capítulo 4). La mortalidad del paíño debida a depredación por gaviota patiamarilla en la isla de Benidorm se estimó en un 16% (Capítulo 4). En un futuro sería interesante explorar la influencia de variables ambientales (como las oceanográficas) en la supervivencia de esta especie.

A diferencia de los resultados obtenidos por Tavecchia et al. (2008) no encontramos grandes diferencias en la supervivencia adulta del paíño en las dos colonias de Benidorm. Las estimas de supervivencia adulta en la colonia 2 de Benidorm durante los primeros años de estudio fueron más bajas y mucho menos precisas que las de la colonia 1 (Capítulo 1, Tavecchia et al. 2008). Durante los

últimos años de estudio (no incluidos en el trabajo de Tavecchia et al. 2008) las dos colonias de Benidorm mostraron una mayor sincronía en parámetros demográficos como la supervivencia o el éxito reproductor (Capítulos 1, 2 y 3). Los modelos de supervivencia que no incorporaron diferencias entre colonias presentaron menos parámetros que los modelos con supervivencia colonia-dependiente. El hecho de que las diferencias de supervivencia entre ambas colonias disminuyeran durante los últimos años de estudio podría ser el responsable de que los modelos más simples fueran seleccionados en términos de parsimonia (Capítulos 2 y 3). Del mismo modo observamos que la concentración al final del periodo de estudio de las observaciones de los individuos que reclutaron en Benidorm, especialmente en la colonia 2, podría ser la causa de que las estimas de supervivencia de estos grupos de individuos sean más altas que las del gupo de individuos de edad desconocida (cuyas observaciones se reparten de forma más homogenea durante todo el periodo de estudio). Estas "diferencias" en las estimas de supervivencia obtenidas en distintos modelos ponen de manifiensto la importancia del monitoreo a largo-plazo en especies longevas.

En las colonias de paíño europeo de la isla de Benidorm se observó un efecto positivo de la experiencia reproductora en la supervivencia local, lo que sugiere que las aves de menor calidad podrían pagar un coste tras la primera reproducción (Capítulo 3). De hecho, se observó una relación positiva entre el éxito reproductor y la supervivencia futura, especialmente entre los individuos con experiencia reproductora.

El éxito reproductor

Tan sólo se ha podido estimar el éxito reproductor en las colonias de Benidorm, ya que el seguimiento en red o una única visita anual a los nidos (métodos empleados en el resto de colonias) no permite la estimación de este parámetro (Capítulos 1 y 2). El éxito reproductor varió anualmente (Capítulo 2 y 4) y aumentó tras el control selectivo de gaviotas patiamarillas depredadoras (Capítulo 4). A pesar de que la depredación influye en este parámetro, las variaciones interanuales detectadas sugieren que factores ambientales climáticos directos (e.g. frecuencia de temporales) o indirectos (e.g. a través de procesos en las cadenas tróficas del tipo *bottom-up*, es decir, la disponibilidad de alimento) podrían estar regulando la productividad de las

colonias de paíño europeo. Estos son factores a explorar en un futuro ya que las variaciones en el éxito reproductor del paíño europeo podrían reflejar condiciones de medio, especialmente de los primeros eslabones de la cadena trófica, convirtiéndose esta especie en un buen bioindicador de especies marinas de nichos tróficos intermedios.

Al igual que sucede con la supervivencia, se observó que el éxito reproductor aumentaba con la edad (Capítulo 2), lo que podría reflejar tanto la adquisición de esperiencia y coordinación con la pareja en la reproducción como la desaparición de individuos de baja calidad en clases de edad jóvenes por presiones de selección (Capítulo 3).

A nivel poblacional, las parejas con experiencia reproductora presentaron un éxito reproductor superior al de parejas noveles (Capítulo 3). De igual forma, a nivel individual la adquisición de experiencia reproductora resultó en un aumento del éxito reproductor posterior (Capítulo 3). Este efecto también podría estar relacionado con la progresiva desaparición de los individuos de baja calidad en la población, sujetos a las mismas presiones de selección mencionadas anteriormente.

LOS COMPROMISOS EVOLUTIVOS

Los organismos longevos podrían modular su esfuerzo reproductor para maximizar su eficacia biológica (*fitness*). En nuestro caso de estudio, no observamos una relación negativa entre el esfuerzo reproductor (entendido como éxito reproductor) y la supervivencia futura (Capítulo 3). La calidad individual podría estar enmascarando este compromiso evolutivo (*trade-off*) ya que los individuos de mayor calidad podrían invertir un menor esfuerzo en la reproducción que los individuos de baja calidad para lograr el mismo éxito reproductor. Sin datos experimentales, imposibles de obtener debido al carácter vulnerable de esta especie, y/o de medidas independientes que pudieran reflejar la calidad individual, nos es imposible desentrañar el potencial efecto de esfuerzo y de la calidad. Puede que los individuos únicamente modulen su inversión en la reproducción ante condiciones ambientales desfavorables, por procesos no-lineales con valores umbrales. Sería interesante explorar esta posibilidad

incluyendo en la modelización índices que pudieran reflejar las condiciones del medio, así como incluir un efecto del individuo para reflejar la potencial heterogeneidad de la calidad individual.

MODELIZACION DE LAS POBLACIONES ESTRUCTURADAS Y CONSERVACIÓN BASADA EN EVIDENCIAS

Los modelos de poblaciones estructuradas construídos a partir de las estimas edad-dependientes de supervivencia y fecundidad mostraron que diferentes combinaciones de parámetros demograficos podían traducirse en tasas de crecimiento poblacional esperadas similares (Capítulo 2). Se puso de manifiesto la importancia de considerar la heterogeneidad espacio-temporal de los rasgos de vida a la hora de realizar proyecciones poblacionales. Los modelos realizados se basaron en estimas obtenidas mediante el análisis de las historias de captura de individuos con edad conocida, no pudimos incluir la productividad de Marettimo por no tener datos ni tampoco se incluyeron efectos temporales en ninguno de los parámetros demográficos. Por tanto, el modelo realizado fue tan sólo una aproximación "sencilla" en base a la información disponible. Probablemente, las poblaciones analizadas no presenten la tasa de crecimiento poblacional estimada, pero el análisis de sensitividad indica que el parámetro clave para la persistencia de la especie es la supervivencia adulta. Ante valores de supervivencia adulta similares a los de la colonia 1 de Benidorm, los gestores de conservación deberían plantearse llevar a cabo estrategias para aumentar dicho parámetro, puesto que no se asegura la persistencia de la población sin el efecto tamponador de la inmigración. En un futuro podrían realizarse modelos en base a estimas más robustas obtenidas tras la recolección de más datos, o modelos que incluyeran efectos de la estocasticidad ambiental y demográfica.

En esta tesis se ha evaluado la efectividad de un plan de conservación del paíño europeo basado en la información obtenida tras muchos años de monitoreo. La estimación de parámetros demograficos en varias colonias de cría gracias a los datos obtenidos de seguimiento individual (Oro et al. 2005, Capítulos 1 y 2) permitió evidenciar que el paíño en Benidorm presentaba una supervivencia reducida para una especie longeva y menor a la de colonias donde la depredación por parte de gaviotas

patiamarillas es supuestamente baja. Dado que la supervivencia adulta fue el parámetro al que la tasa de crecimiento esperada de la población mostró una mayor sensitividad (Capítulo 2), el manejo de la población de gaviotas patiamarillas se programó con el objetivo de reducir la mortalidad del paíño debida a depredación. El estudio de la interacción entre ambas especies permitió limitar el descaste de gaviotas a aquellos individuos especialistas, resultando ser una medida efectiva y eficiente a la hora de incrementar la supervivencia y fecundidad de la presa. Este trabajo refleja la importancia y efectividad de la planificación de las actuaciones de conservación basada en evidencias (Capítulo 4). Dado que los recursos en conservación son limitados, una buena planificación es crucial para optimizarlos.

Conclusiones

1. En este proyecto de tesis se propuso el objetivo de obtener información de carácter ecológico, evolutivo, y aplicada al manejo de poblaciones naturales, a partir del análisis estadístico de datos individuales recogidos mediante estudios a largo plazo en varias poblaciones de paíño europeo. Una primera conclusión es la demostración de la necesidad de establecer protocolos de monitoreo de poblaciones en base a los parámetros de interés y la precisión deseada.

2. Los métodos de captura en red propiciaron un mayor número de capturas pero no de recapturas, e incrementaron la proporción de individuos transeúntes capturados con respecto a la captura en nidos. Independientemente del metodo utilizado, todos los protocolos permitieron obtener estimas de supervivencia adulta, pero no de tamaño poblacional.

3. La presencia de individuos transeuntes fue un rasgo habitual en todas las colonias de paíño europeo estudiadas. La presencia de una porción de individuos que desaparecen de la población tras la primera captura puede ser un rasgo habitual en las poblaciones de paíño y de aves marinas en general. La proporción de individuos reproductores transeúntes (i.e. no prospectores) presentes en una población puede tener importantes consecuencias en la dinámica y persistencia de las poblaciones.

4. El porcentaje de individuos marcados como pollos que reclutó en las colonias de estudio fue muy bajo. A pequeña escala espacial estos individuos mostraron tendencias filopátricas.

5. La edad de la primera reproducción y los patrones de reclutamiento del paíño variaron a diferentes escalas geográficas. No se encontró una explicación evidente para dicho fenómeno.

6. La supervivencia adulta mostró variaciones espacio-temporales importantes. Se comprobó que, al igual que el éxito reproductor, aumentó tras la reducción de la depredación causada por gaviotas patiamarillas especialistas en el entorno de las colonias de cría. Tasas de supervivencia bajas (entorno al 0.8) pueden ser un síntoma de que una determinada población está en peligro sino acude al rescate el efecto de la inmigración.

7. Se observó un incremento en las probabilidades de supervivencia y en la productividad de los individuos con la edad y la adquisición de experiencia reproductora. Se detectó una relación positiva entre el éxito reproductor y la supervivencia futura, que probablemente respondió a la progresiva desaparición por presiones de selección de los individuos jóvenes de baja calidad.

8. La reproducción resultó costosa en términos de supervivencia para los individuos inexpertos. No se encontró ningún coste asociado al esfuerzo reproductor, expresado en términos de éxito reproductor.

9. Las tasas de crecimiento poblacional esperado estimadas mostraron la mayor sensitividad a cambios en la supervivencia adulta, de acuerdo a lo esperado para especies longevas.

10. El descaste selectivo de gaviotas especialistas basado en evidencias previas resultó ser una medida efectiva y eficiente para la conservación del paíño.

11. De los estudios realizados en esta tesis se desprende la necesidad de integrar el estudio de factores metodológicos, ecológicos y evolutivos en los trabajos de conservación y manejo de poblaciones.

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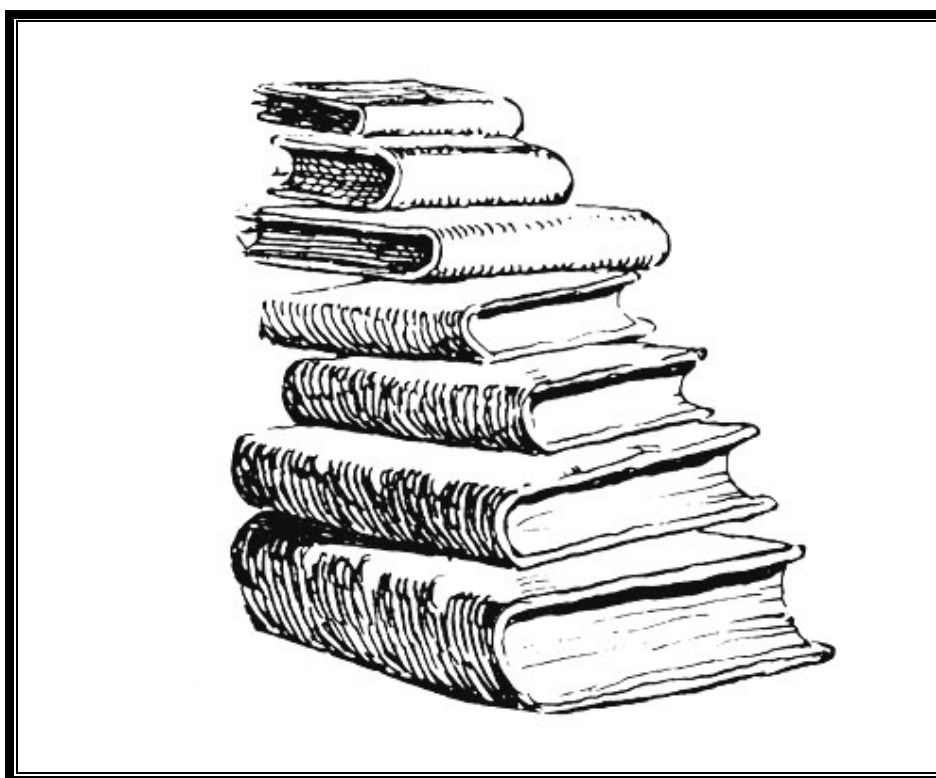
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