Agreement on the Conservation of Albatrosses and Petrels

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Drivers of age at first reproduction in the wandering albatross (*Diomedea exulans*): Demographic factors, environmental conditions and sex-specific responses

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SUMMARY

Age at first reproduction is an important life-history trait that marks the beginning of reproductive allocation in long-lived organisms and drives patterns of life-history strategies. Demographic factors and environmental conditions likely affect age at first reproduction through multiple pathways: food resources availability and energy storage from birth to recruitment, competition for breeding sites, and mate availability. Using a unique 35-year dataset of individual-based mark-recapture data from a wandering albatross (*Diomedea exulans*) population at Crozet (southern Indian Ocean), we investigated how demographic factors and environment influence age at first reproduction. The population experienced major fluctuations, declining by 50% in the 1970s before partially recovering in the 1980s. It was also exposed to important environmental changes, including variations in large-scale climate phenomena and changes in subtropical anticyclone systems like the Mascarene high pressure system. We investigated how demographic factors and environmental conditions influenced age at first reproduction through their effects on survival and breeding probabilities. Age at first reproduction declined across cohorts for both sexes from 1970 to the mid-1980s, then stabilized. Females recruited at 9.0 years in early cohorts versus 7.5 years in later ones; males declined from 10.2 to 9.2 years. Environmental conditions at birth, particularly the El Niño Southern Oscillation and the Mascarene high, influenced recruitment timing through delayed effects of natal condition on breeding probability rather than survival. Mate availability strongly facilitated earlier recruitment in both sexes, while natal population density delayed male recruitment specifically. Recruitment timing in wandering albatrosses is shaped primarily by developmental programming during the natal period rather than by immediate environmental triggers at sexual maturity, with mate availability and population density modulating these early-life effects in sex-specific ways.

Given that recruitment is an important life-history event linked to population-level reproductive rates, accurate demographic projections require models accounting for cohort-specific effects under changing environments.

RECOMMENDATIONS

1. We recommend maintaining long-term monitoring for Albatross populations, and more generally all type of long-term ecological research.
2. We advocate for demographic studies as they showcase the result of management strategy at the level of life history traits.
3. We urge continued and strengthened efforts to reduce seabird bycatch in fisheries, particularly for female wandering albatrosses. Our results show that female-biased fishery mortality delays male recruitment, with cascading effects on population reproductive rates.
4. We recommend that population projection models used for conservation assessments incorporate cohort-specific recruitment effects and account for early-life environmental conditions, rather than assuming constant age at first reproduction.
5. We highlight that sex-specific demographic monitoring (including tracking of operational sex ratios and mate availability) should be integrated into routine population assessments for ACAP-listed species, as sex-biased perturbations generate complex recruitment dynamics that cannot be detected from aggregate population counts alone.

Impulsores de la edad de la primera reproducción en ejemplares de *Diomedea exulans*: factores demográficos, condiciones ambientales y respuestas específicas por sexo

RESUMEN

La edad de la primera reproducción es un rasgo importante de la historia de vida que marca el comienzo de la asignación reproductiva en organismos de larga vida e impulsa los patrones de estrategias de historia de vida. Los factores demográficos y las condiciones ambientales probablemente afecten la edad de la primera reproducción de múltiples maneras: por la disponibilidad de recursos alimenticios y el almacenamiento de energía desde el nacimiento hasta el reclutamiento, la competencia por los sitios reproductivos y la disponibilidad de parejas. Utilizando un conjunto de datos único, de 35 años de datos de marcaje y recaptura basados en ejemplares de una población de *Diomedea exulans* en Crozet (Océano Índico meridional), investigamos cómo los factores demográficos y el medioambiente influyen en la edad de la primera reproducción. La población experimentó grandes fluctuaciones: disminuyó un 50 % en la década de 1970 y se recuperó parcialmente en la década de 1980. También estuvo expuesta a importantes cambios ambientales, incluidas variaciones en fenómenos climáticos a gran escala y cambios en sistemas de anticiclones subtropicales como el sistema de alta presión de las islas Mascareñas. Investigamos cómo los factores demográficos y las condiciones ambientales

influyeron en la edad de la primera reproducción a través de sus efectos en la supervivencia y las probabilidades de reproducción. Entre 1970 y mediados de la década de 1980, la edad de la primera reproducción en ambos sexos disminuyó en todas las cohortes, y luego se estabilizó. Las hembras se reclutaron a los 9,0 años en las primeras cohortes frente a 7,5 años en las posteriores; por su parte, la edad de reclutamiento de los machos disminuyó de 10,2 a 9,2 años. Las condiciones ambientales al nacer, en particular el patrón climático El Niño-Oscilación del Sur (ENOS) y el fenómeno de alta presión conocido como anticiclón de Mascareñas, influyeron en el momento del reclutamiento por los efectos retrasados de la condición natal en la probabilidad de reproducción más que en la supervivencia. La disponibilidad de parejas facilitó considerablemente la aceleración de reclutamiento en ambos sexos, mientras que la densidad de población natal retrasó específicamente el reclutamiento de los machos. El momento del reclutamiento en los ejemplares de *Diomedea exulans* está determinado principalmente por la programación del desarrollo durante el período natal más que por los desencadenantes ambientales inmediatos en la madurez sexual, y la disponibilidad de parejas y la densidad de la población modulan estos efectos tempranos de manera distinta para cada sexo. Dado que el reclutamiento es un evento importante de la historia de vida vinculado a las tasas reproductivas a nivel de la población, para que las proyecciones demográficas sean precisas se requieren modelos que tengan en cuenta los efectos específicos para cada cohorte en entornos cambiantes.

RECOMENDACIONES

1. Recomendamos mantener el monitoreo a largo plazo de las poblaciones de albatros y, de manera más general, de todo tipo de investigación ecológica a largo plazo.
2. Abogamos por la realización de estudios demográficos, ya que muestran el resultado de la estrategia de gestión a nivel de rasgos de la historia de vida.
3. Instamos a continuar y fortalecer los esfuerzos para reducir la captura secundaria de aves marinas, en particular de las hembras de *Diomedea exulans,* en las pesquerías. Nuestros resultados muestran que la mortalidad por pesquerías sesgada hacia las hembras retrasa el reclutamiento de los machos, lo que genera efectos en cascada en las tasas reproductivas de la población.
4. Recomendamos que los modelos de proyección de población utilizados para las evaluaciones de conservación incorporen efectos de reclutamiento específicos para cada cohorte y tengan en cuenta las condiciones ambientales de la primera etapa de la vida en lugar de presuponer una edad constante de la primera reproducción.
5. Destacamos que el monitoreo demográfico específico para cada sexo (incluido el seguimiento de las proporciones operativas de sexo y la disponibilidad de parejas) debe integrarse a las evaluaciones de rutina de la población para las especies incluidas en la lista del ACAP, ya que las perturbaciones sesgadas por el sexo generan dinámicas de reclutamiento complejas que no se pueden detectar solo con recuentos agregados de la población.

Facteurs déterminant l'âge de la première reproduction chez le *Diomedea exulans* : Facteurs démographiques, conditions environnementales et réponses spécifiques au sexe

RÉSUMÉ

L'âge à la première reproduction est un trait important du cycle de vie, qui marque le début de l'effort de reproduction chez les organismes à longue durée de vie et détermine les schémas des stratégies de cycle de vie. Les facteurs démographiques et les conditions environnementales affectent probablement l'âge de la première reproduction de multiples manières : disponibilité des ressources alimentaires et stockage de l'énergie de la naissance au recrutement, compétition pour les sites de reproduction et disponibilité des partenaires. En utilisant un jeu de données individuelles uniques de marquage-recapture, collecté sur 35 ans pour une population de *Diomedea exulans* à Crozet (au sud de l'océan Indien), nous avons étudié comment les facteurs démographiques et l'environnement influencent l'âge à la première reproduction. La population a connu d'importantes fluctuations, diminuant de 50 % dans les années 1970 avant une récupération partielle dans les années 1980. Elle a également été exposée à d'importants changements environnementaux, notamment des variations des phénomènes climatiques à grande échelle et des changements dans les systèmes anticycloniques subtropicaux comme l'anticyclone des Mascareignes. Nous avons étudié comment les facteurs démographiques et les conditions environnementales influençaient l'âge à la première reproduction à travers leurs effets sur les probabilités de survie et de reproduction. L'âge à la première reproduction a diminué dans toutes les cohortes pour les deux sexes de 1970 au milieu des années 1980, puis s'est stabilisé. Les femelles étaient recrutées à 9,0 ans pour les premières cohortes contre 7,5 ans pour les suivantes ; les mâles ont vu leur âge diminuer, passant de 10,2 à 9,2 ans. Les conditions environnementales à la naissance, en particulier El Niño-oscillation australe et l'anticyclone des Mascareignes, ont influencé le calendrier de recrutement par le biais des effets différés des conditions natales sur la probabilité de reproduction plutôt que sur la survie. La disponibilité de partenaires a beaucoup facilité un recrutement plus précoce chez les deux sexes, tandis que la densité de population natale a retardé spécifiquement le recrutement des mâles. Le calendrier de recrutement du *Diomedea exulans* est davantage influencé par la programmation développementale durant la période natale que par des déclencheurs environnementaux immédiats au moment où la maturité sexuelle est atteinte. La disponibilité des partenaires et la densité de population modulent ces effets aux premiers stades de la vie de manière spécifique au sexe. Le recrutement est un événement important du cycle de vie, lié aux taux de reproduction au niveau de la population : des modèles tenant compte des effets spécifiques à chaque cohorte dans des environnements changeants sont donc nécessaires pour des projections démographiques précises.

RECOMMANDATIONS

1. Nous recommandons le maintien d'un suivi à long terme des populations d'albatros, et plus généralement de tout type de recherche écologique à long terme.

2. Nous préconisons des études démographiques, capables de mettre en évidence les résultats de la stratégie de gestion au niveau des caractéristiques de l'histoire de vie.

3. Nous insistons sur la nécessité de poursuivre et de renforcer les efforts visant à réduire les captures accessoires d'oiseaux marins dans les pêcheries, en particulier pour les *Diomedea exulans* femelles. Nos résultats indiquent que la mortalité liée aux pêcheries, plus fréquente chez les femelles, retarde le recrutement des mâles, avec des effets en cascade sur les taux de reproduction de la population.

4. Nous recommandons que les modèles de projection démographique utilisés pour les évaluations de conservation intègrent les effets de recrutement spécifiques à chaque cohorte et tiennent compte des conditions environnementales aux premiers stades de la vie, plutôt que de supposer un âge constant à la première reproduction.

5. Nous soulignons que le suivi démographique spécifique au sexe (notamment le suivi des sex-ratios opérationnels et de la disponibilité des partenaires) devrait être intégré aux évaluations démographiques de routine pour les espèces inscrites à l'ACAP, car les perturbations dépendantes du sexe génèrent une dynamique de recrutement complexe impossible à détecter à partir des seuls recensements de population agrégés.

1. INTRODUCTION

Age at first reproduction, or recruitment, marks an important transition in an organism's life and is a core trait in life-history theory (Aubry et al., 2009; Stearns, 1992). The timing of first reproduction is central to a fundamental trade-off in life histories: balancing the benefits of early reproduction against the costs of reduced survival or future reproductive success (Roff, 1993). This trait determines not only when individuals begin contributing to population growth but also influences the entire trajectory of their reproductive life. At the population level, age at first reproduction drives population dynamics and contributes to population growth rate. Even small changes in this parameter may substantially affect population viability, particularly in long-lived species where generation times are extended (Jenouvrier et al., 2015).

Age at first reproduction is influenced by conditions experienced throughout an individual's pre-reproductive lifetime. Early-life conditions can have lasting consequences through developmental programming, where environmental conditions during critical developmental periods influence adult traits and performance (Gluckman et al., 2005). When favorable conditions enhance lifelong performance, these effects are often referred to as the "silver spoon effect", manifesting as permanent changes in physiology, behavior, or morphology that influence both survival and reproductive timing. Conversely, adverse early conditions may result in developmental constraints that reduce reproductive potential throughout life (Metcalfe and Monaghan, 2001).

The wandering albatross (*Diomedea exulans*) population at Crozet (46°S; 52°E, southern Indian Ocean) represents an excellent opportunity to investigate the drivers of age at first reproduction variation in a long-lived species. This population has been monitored for over five decades with extensive individual-based data (Weimerskirch, 2018). A sharp population decline (loss of 50% of the breeding population) was documented from 1970 until mid-1980s, followed by a steady increase (Delord et al., 2008). Previous studies documented fluctuations in age at first reproduction across cohorts, with a decrease from 12 to 10 years between 1966 and 1982. This decrease was hypothesized to result from reduced population density, which lowered competition for food resources. However, no formal quantitative study had investigated the demographic and environmental drivers of these changes in recruitment patterns.

In this study, we investigate the drivers of age at first reproduction variation in the wandering albatross population at Crozet, using a unique 35-year individual-based mark-recapture dataset covering 11,166 individuals (5,604 males and 5,562 females) ringed as chicks between 1970 and 2005. We tested five primary, non-mutually exclusive hypotheses: (H1) density-dependent effects at birth, (H2) density-dependent effects at recruitment through mate availability, (H3) environmental effects at birth consistent with silver spoon effects, (H4) environmental effects at recruitment as proximate breeding cues, and (H5) sex-specific responses to demographic and environmental conditions.

2. RESULTS

2.1. Temporal changes in age at first reproduction

Capture-recapture analysis revealed clear temporal patterns in age at first reproduction, with a decline from 9 to 7.8 years in females, and from 10.5 to 9.2 in males, followed by an increase to 8.2 and 9.8 years respectively by 2005. Males consistently began breeding about one year later than females throughout the study period.

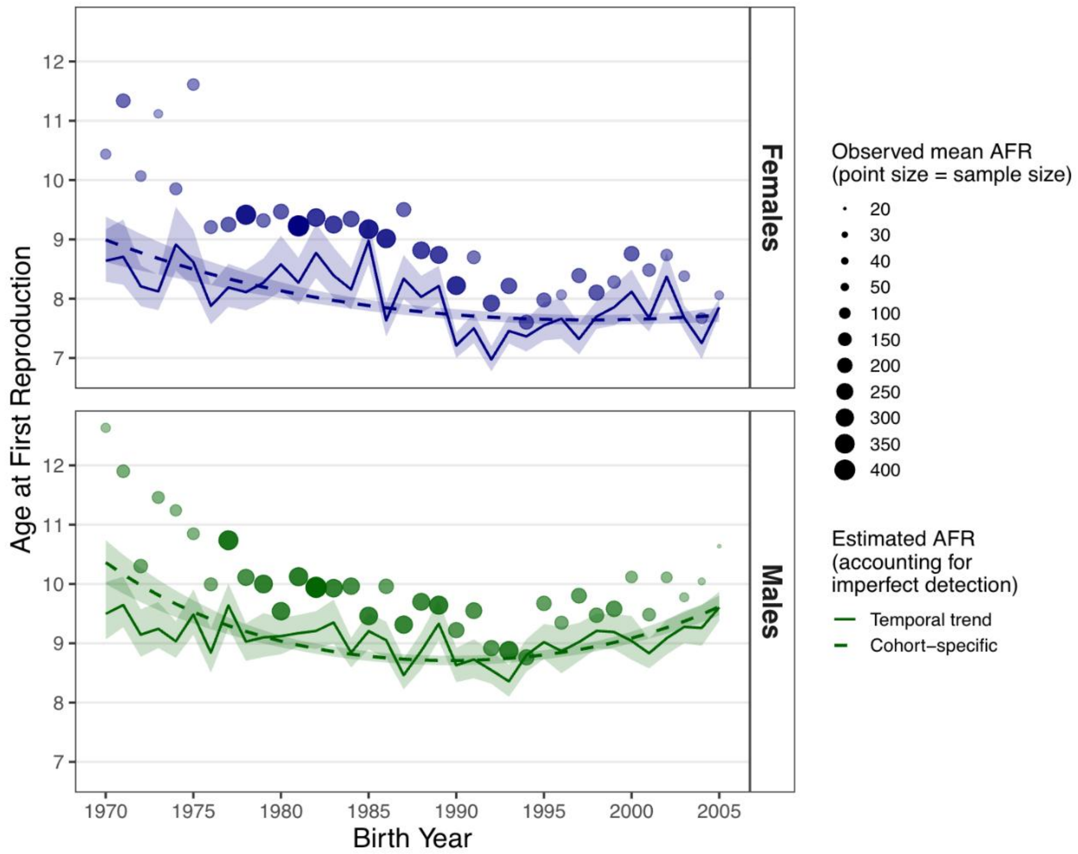

Figure 1: Temporal patterns in age at first reproduction. Age at first reproduction (AFR in legends) for male and female cohorts from 1970 to 2005. Points represent observed mean age at first reproduction from raw data, with point size and transparency proportional to sample size (n ranging from 22 to 426 individuals per cohort-sex combination). Smaller, more transparent points indicate cohorts with limited data, particularly in early years. Lines show model estimates from capture-recapture analysis that account for imperfect detection: dashed lines represent temporal trends while solid lines show cohort-specific effects, with 95% credible intervals (shaded areas). Both observed points and model estimates share the same Y-axis scale (in years). Discrepancies between observed points and model estimates, especially in early cohorts with small sample sizes, reflect imperfect detection and sampling limitations that are corrected by the capture-recapture framework.

2.2. Effects of demographic factors

There were consistent positive effects of mate availability on breeding probability for pre-breeders of ages 6 to 15, for both sexes across multiple time lags. Higher mate availability was consistently associated with earlier breeding. Population density at birth had a negative effect on breeding probability for males but not for females, indicating that high natal population density may constrain male offspring development through intensified competition for resources.

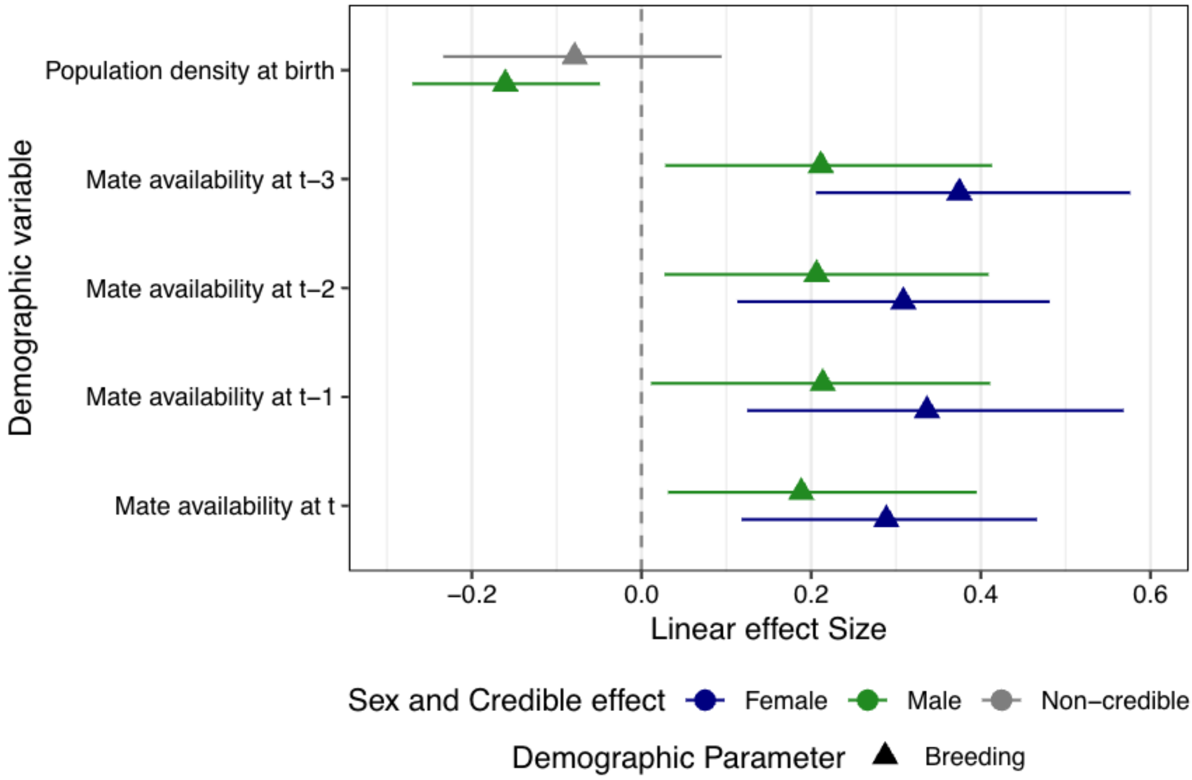

Figure 2: Effects of population density and mate availability on breeding probability of pre-breeders. Linear effect sizes of mate availability are evaluated at different time lags (t to t-3) and population density at birth. Blue and green triangles represent credible effects for females and males, respectively, while gray indicates non-credible effects. Error bars show 95% credible intervals.

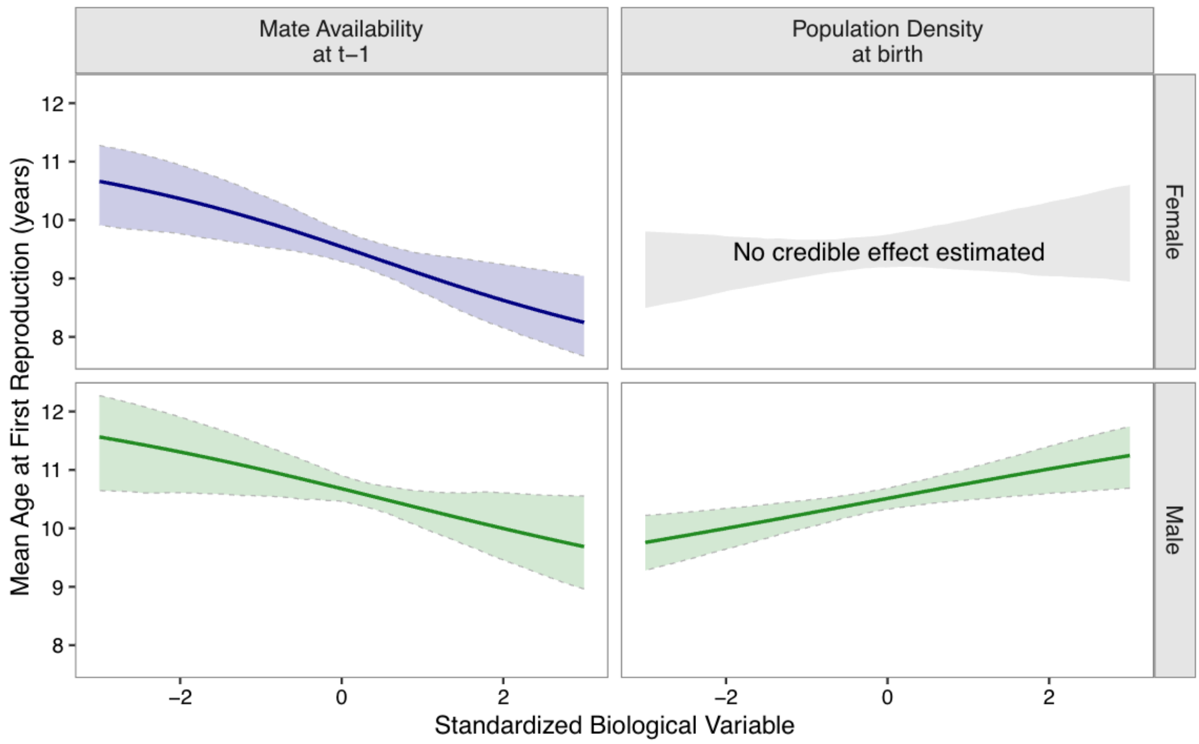

Figure 3: Effects of demographic variables on age at first reproduction. The figure shows the effect of standardized mate availability at t-1 and population density at birth on mean age at first reproduction

for females (top row, blue) and males (bottom row, green). Solid lines represent mean effects, with shaded areas indicating 95% confidence intervals. Only mate availability at t-1 is shown, as results were similar for each time lag. Population density at birth effect on female age at first reproduction was not credible. It is displayed in grey to contrast with credible effects.

2.3. Effects of environmental conditions

Only environmental conditions experienced at birth yielded credible effects on vital rates. ENSO conditions at birth showed the strongest influence, with positive effects on breeding probabilities of both females and males. Mascarene high magnitude at birth also had a positive credible effect on breeding probabilities for both sexes. In contrast, no environmental variables experienced at recruitment showed credible effects on either breeding probability or survival for either sex. This asymmetry between early-life and current environmental effects suggests that recruitment timing in this long-lived seabird is shaped primarily by developmental programming during the natal period rather than by immediate environmental triggers at sexual maturity.

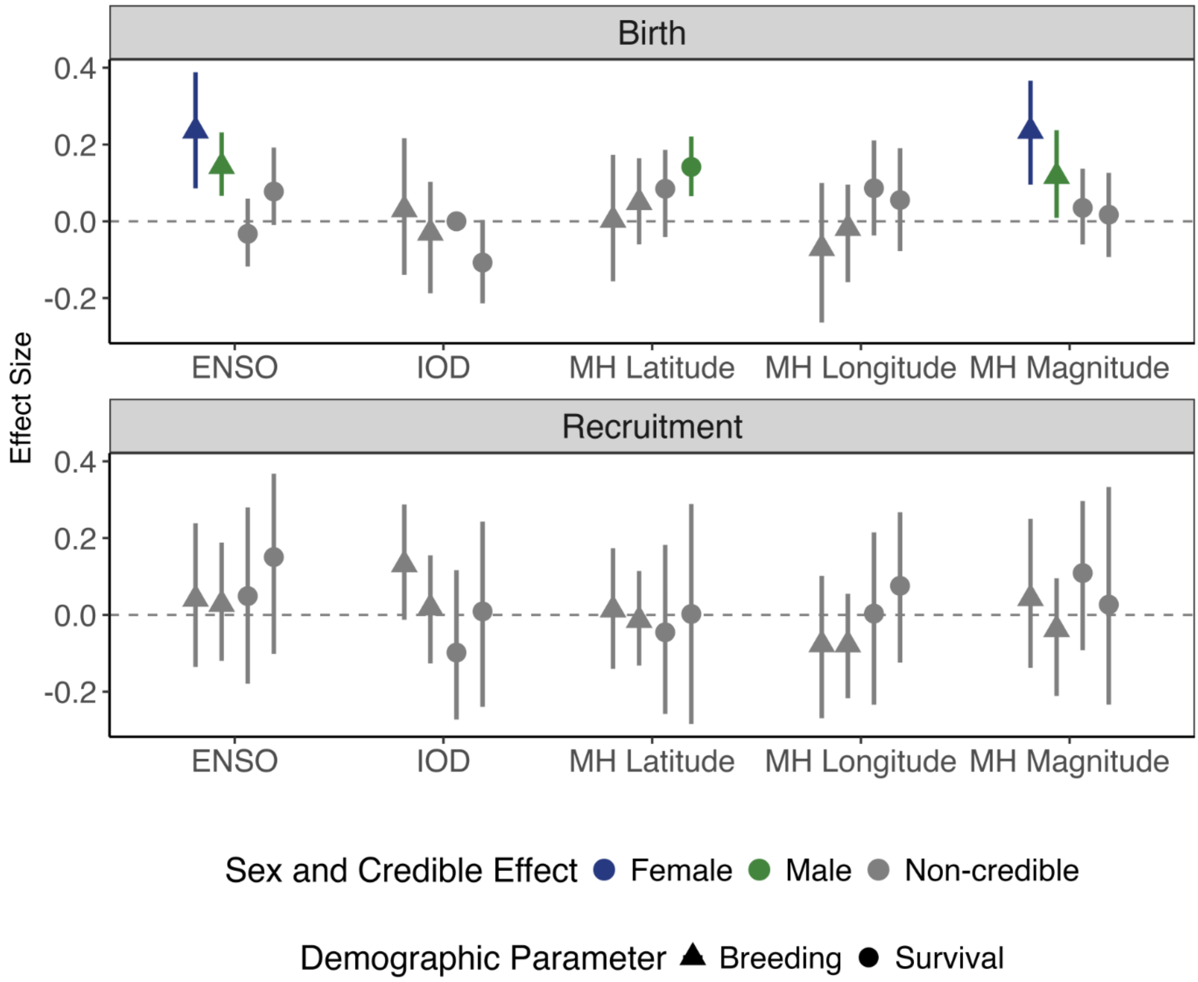

Figure 4: Effects of environmental variables on survival and breeding probabilities of pre-breeder wandering albatrosses. Effects of five environmental variables: Indian Ocean Dipole (IOD), El Niño Southern Oscillation (ENSO), and three Mascarene high metrics (latitude, longitude, and magnitude), tested at birth (top) and recruitment (bottom) show the temporal window during which these covariates influence vital rates. Points show mean effects with 95% credible intervals. Credible effects (intervals excluding zero) are in blue for females and green for males. Triangles indicate breeding probability, circles indicate survival.

3. DISCUSSION

Natal population density affected male, but not female, recruitment timing. In wandering albatrosses, males are larger and mature later than females, requiring greater body mass to initiate breeding. High natal population density may constrain offspring development through intensified intraspecific competition for resources. Males, with their higher energetic requirements during the extended rearing period, may be more vulnerable to resource limitation when competition is intense. Females, with their lower weight threshold for breeding onset and earlier maturation, appear buffered against such density effects during development.

Mate availability strongly influenced recruitment timing, with effects apparent across multiple time lags (t to $t-3$). This multi-year lagged effects likely reflect the extended pair formation process, which takes on average 3.2 years for males and 2.3 years for females. The male-biased operational sex ratio, driven by female-biased fishery mortality, creates asymmetric mating opportunities that further delay male recruitment. Males, facing stronger intrasexual competition for the limited pool of females, experience longer pair formation periods.

Environmental conditions at recruitment showed no effect on age at first reproduction, in stark contrast to natal conditions. Yet environmental conditions experienced at birth determined when individuals bred for the first time. This asymmetry supports the developmental programming hypothesis, whereby early experiences create lasting phenotypic effects that override immediate environmental triggers. These results align most closely with the silver spoon hypothesis: favorable early-life conditions conferred lifelong advantages, with individuals experiencing beneficial natal environments recruiting earlier regardless of conditions at sexual maturity.

4. BROADER IMPLICATIONS

These findings have important implications for predicting population responses to environmental change. Because natal conditions (not recruitment-period conditions) determine when individuals breed, cohorts experiencing poor environmental conditions during development will show delayed recruitment years later, regardless of conditions when they reach maturity. In wandering albatrosses, where individuals recruit at 7–10 years on average and can delay first reproduction up to 15 years, such cohort effects persist for over a decade, creating lagged demographic responses to environmental perturbations. Sex-biased mortality from fisheries further complicates predictions by altering mate availability and generating sex-specific recruitment delays. Understanding recruitment therefore requires tracking environmental conditions, demographic structure, and their interactions across the entire pre-breeding period, a challenge for species experiencing rapid environmental change in increasingly human-impacted oceans.

5. REFERENCES

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