

JOURNAL OF AVIAN BIOLOGY

Article

Energetic constraints drive sex-specific parental care in the monomorphic Leach's storm-petrel *Hydrobates leucorhous*

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Journal of Avian Biology

2022: e02904

doi: 10.1111/jav.02904

Subject Editor:

Judy Shamoun-Baranes

Editor-in-Chief: Jan-Åke Nilsson

Accepted 29 December 2021



Sex-specific parental care in dimorphic species may be unsurprising, but why this occurs in monomorphic species is more puzzling. To date, however, there have been few examinations of the causes of this phenomenon. Here, we evaluated possible explanations of sex-specific provisioning in the monomorphic Leach's storm-petrel *Hydrobates leucorhous* (until recently *Oceanodroma leucorhoa*). We tracked the chick-rearing behavior of 74 mated pairs using an automated nest monitoring system and collected daily measurements of chick growth. We found that males provisioned more frequently and made a larger overall contribution to chick feeding than females. Within-individual trip duration was more variable for females, suggesting that they were alternating to a greater degree between short, energetically taxing trips that prioritize chick care and longer, recovery trips that prioritize self-care. Moreover, females were more likely to embark on longer trips after completing a short trip and after encountering a chick in good condition. Males, however, appeared better able to perform repeated short trips that resulted in more frequent provisioning as well as greater amounts overall. These findings are consistent with the explanation that energetic constraints on females give rise to male-biased, sex-specific provisioning in a monomorphic species and are likely to explain similar patterns in other long-lived species where adult survival is high.

Keywords: Leach's storm-petrel, monomorphic seabird, parental care, sex-specific provisioning

Introduction

Animals have evolved a diversity of traits to benefit offspring fitness. Any such trait, morphological or behavioral, which increases offspring fitness is considered parental care (Clutton-Brock 1991). The degree and forms of parental care are the product of ecological constraints and coevolve with a species' life-history traits (Wedell et al. 2006, Balshine 2012). For example, general traits such as high egg mortality, slow egg maturation, low juvenile survival or low adult death rates are all expected to select for greater parental care over evolutionary time (Table 2 in Klug and Bonsall 2010). As such, there are broad patterns in the forms of parental care observed across vertebrate



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taxonomic groups. In most groups, female-only care or no care are most commonly observed (Reynolds et al. 2002).

Birds, however, are the exception where biparental care is found in over 85% of species (Cockburn 2006). Yet even in avian species with biparental care, sexes often contribute care in varying degrees and ways (Wesolowski 1994). One explanation for this variation is sexual conflict, which leads each partner to manipulate their level of care to maximize long-term fitness, potentially at the expense of their partner (Houston and Davies 1985). The relative level of care invested by each sex may depend on a variety of factors including individual quality, residual reproductive value and degree of extrapair paternity (Wedell et al. 2006). Thus, the amount invested by each sex is dynamic and will vary with the individual characteristics of each parent. Differential investment by each sex may also be more systematic with one sex adopting particular breeding duties, e.g. in raptors, females typically incubate while males hunt (Sonerud et al. 2014). In fact, some degree of role specialization is observed in most avian species and is typically linked with dimorphism (Barta et al. 2014). For example, incubation in birds is commonly sex-specific, with one sex taking on most of the responsibility. Many dimorphic species, however, also unequally share provisioning duties. Sex-specific provisioning has been most widely studied in seabirds where improved foraging capabilities of the larger sex are thought to lead to competitive exclusion of the smaller sex at foraging grounds (Lewis et al. 2002, Phillips et al. 2017). Sex-specific provisioning, however, may also occur in the absence of size dimorphism, indicating that other explanations are necessary to account for this phenomenon (Lewis et al. 2002, Thaxter et al. 2009, Burke et al. 2015).

Four non-mutually exclusive mechanisms may explain the occurrence of sex-specific provisioning in monomorphic birds (adapted from Peck and Congdon 2006). The 'nest attendance rhythms hypothesis' states that differences in the timing of nest visits may lead to sex-specific levels of care. This could be caused by differences in daily foraging rhythms (Casaux et al. 2001) or perceived predation risk if one sex is more risk averse (Expósito-Granados et al. 2016). For example, lunar phase is known to affect nest attendance in several seabird species with individuals reducing or delaying nest visits due to elevated predation pressure during periods of increased illumination (Manuwal 1974, Watanuki 1986). If one sex is more responsive to offspring condition, then the 'offspring condition hypothesis' may explain varying levels of care (Kilner 2002). Sex-specific responses to offspring condition might be caused by selection for one sex to more precisely allocate care due to higher overall investment, sexual conflict or as a mechanism for partial compensation of parental care. The 'cryptic dissimilarities hypothesis' proposes that even species categorized as sexually monomorphic may be sufficiently different morphologically to create unequal foraging abilities between males and females, which may in turn lead to competitive exclusion of one sex while foraging, and ultimately divergent parental roles (Peck and Congdon 2006). Lastly, the 'energetic constraints hypothesis' posits that energetic limitations or nutritional requirements may require one

sex to devote more time to self-provisioning or to selectively target particular prey, resulting in longer foraging trips and reduced food delivery to offspring (Gray and Hamer 2001, Welcker et al. 2009). Energetic constraints may arise from asymmetric investment early in the breeding period, such as nest construction and defense (Harris 1966) by one sex or egg production by females, resulting in differential energetic or nutritional demands that are carried over to later breeding stages. Though some studies have explored these hypotheses in isolation, few studies have simultaneously assessed multiple hypotheses in monogamous species with sex-specific parental care.

Among birds, seabirds are notable for displaying obligate biparental care (Cockburn 2006), which is maintained over extended incubation and chick-rearing periods (Burger 1980). Most seabirds are visually monomorphic (Schreiber and Burger 2001), which historically made it challenging for human observers to assign sex-specific behaviors in the field. The proliferation of light-weight tags and molecular sexing has enhanced our ability to collect detailed behavioral observations from a large number of known-sex individuals. In this study, we employed these methods to investigate parental care in the sexually monomorphic Leach's storm-petrel *Oceanodroma leucorhoa*, which displays traits typical of seabirds, such as long life, delayed sexual maturity, social monogamy and low rates of extra-pair paternity (Pollet et al. 2019). This species has previously been described as having male-biased care (Mauck et al. 2011), but this finding came from a single colony and a small number of individuals, so whether this strategy is widespread within the species is unknown. Here, we focused on the extended 55-day provisioning period, during which both sexes undertake multi-day foraging trips to collect food for dependent offspring waiting at the nest (Ricklefs et al. 1985). After evaluating whether male-biased care occurs in this population, we explored the four previously described hypotheses, explicitly testing the three (offspring condition, nest attendance, energetic constraints) that apply to Leach's storm-petrels, to identify the mechanisms that underlie sex-biased parental care in this monomorphic species.

Methods

Study site and field methods

Fieldwork was conducted on Bon Portage Island, Nova Scotia, Canada (43°26'N, 65°45'W), which is home to approximately 39 000 breeding storm-petrel pairs (Pollet and Shutler 2018). A colony of 550 marked burrows has been monitored on Bon Portage Island since 2010. During the 2016 breeding season, we checked marked burrows every five days beginning approximately two weeks before the average hatch date in the monitored portion of the colony, which is 21 July. During burrow checks, breeding adults were removed from the burrow and banded, if not already. From each adult, we collected morphometrics: mass with a Pesola scale (100

± 1 g), flattened wing chord with a metal wing chord ruler (nearest 1 mm), and tarsus length with Mitutoyo digital calipers (150 ± 0.1 mm). Additionally, for chicks we measured the head-bill length (the length from the back of the skull to the tip of the bill) using digital calipers. From previously unbanded birds, we also collected 75 μ l of blood from the brachial vein for molecular sexing. Blood samples were stored at room temperature in 0.5 ml of Queen's lysis buffer. DNA extraction and molecular sexing were conducted using the methods described in Hoover et al. (2018).

After a burrow was checked, we placed a lattice gate of small sticks in front of the burrow entrance. We rechecked burrows only after the lattice gate was disturbed to minimize the likelihood of handling the same breeding adult more than once, which is consistent with a monitoring protocol that has been shown to result in low nest abandonment rates (Blackmer et al. 2004). After we established the identity of the breeding pair within a burrow, all subsequent burrow checks were performed by reaching into the nest cavity to check the status of the nest. This allowed us to determine hatch dates with minimal disturbance to the adults. Once brooding ceased, typically within a few days after hatching, chicks were weighed each day between 1000 and 1300 and morphometrics were taken every three days. Sampling was conducted under the approval of the University of California, Davis Institutional Animal Care and Use Committee Protocol 19288, Canadian Wildlife Service (CWS) Banding permit 10695 and CWS Research permit SC2742.

To record provisioning behavior, we monitored nest attendance patterns using radio-frequency identification (RFID) readers combined with passive integrated transponder (PIT) tags. PIT tags encased in plastic leg bands (EM4102 125 kHz) were attached to the unbanded tarsi of 148 birds during burrow inspections. The weight of the PIT tag and plastic leg band together was 1.2 g, which is approximately 2.5% of the mean weight (46.7 g) of adult Leach's storm-petrels on Bon Portage Island. PIT tags are passive and rely on the electromagnetic field produced by the RFID reader to transmit the unique identification number of the PIT tag. This number is then recorded by the RFID reader along with the detection time. Our RFID system was based on the design described in Bridge and Bonter (2011), but added a second antenna to decrease the possibility of missed detections and to assist with determining whether individuals were entering or exiting a burrow (details given in the Supporting information). We deployed 74 RFID readers at the start of the chick-rearing period and chicks in each of these burrows were measured using the protocol described above. To evaluate the potential impacts of the RFID readers, we compared the mass of similarly aged chicks in 34 control burrows once during the provisioning period (age of control chicks ranged from 19 to 43 days) and compared the age-specific mass of RFID-monitored and control chicks.

Statistical analyses

All statistical analyses were conducted in R ver. 3.5.1 (<www.r-project.org>). When relevant, the assumptions of

normality were assessed by visual inspection of residual plots. Throughout, means are given plus/minus the standard error. Significance was assessed based on an alpha level of 0.05.

We compared two general features of provisioning between each sex: feeding frequency and meal size. Feeding frequency depends entirely on the duration of foraging trips; as such, we used the interval between nest visits, which were rounded to day-long intervals because adults only provision at night and only once per night. During the first week post hatching, adults may brood the chick and remain in the burrow during the day. To exclude these brooding events from our analyses of provisioning behavior, we used RFID detection sequences to classify whether individuals were entering or exiting a burrow and thus brooding or foraging, respectively (see the Supporting information for details of the classification procedure). Meal size was calculated based on the 24-h change in chick mass (g). Total provisioning amount was also calculated for each individual as the sum of all meals delivered by that individual. We excluded nights when both parents provisioned as the individual contribution could not be determined.

To evaluate whether trip duration (and hence provisioning frequency) differed between males and females, we calculated the average trip duration for each individual and compared this response variable between the sexes using a linear model (LM). The average trip duration from each individual was weighted by the number of trips taken by that individual. To evaluate the impact of sex on provisioning amount, linear mixed-effect models (LMMs) were fit using the lme4 package (Bates et al. 2012). We first developed a global model of daily mass change as a function of chick mass, chick age, parent sex and trip duration as fixed effects (as well as all two-way interactions) and adult identity (band number) as a random effect. All sub-models were then generated and compared using Akaike's information criteria (AIC) to identify the top model.

Leach's storm-petrels are nocturnal at the breeding colony and predation risk by owls and gulls may vary with lunar phase leading to altered provisioning behavior if one sex is more risk averse (Watanuki 1986). To evaluate whether sexes displayed distinct provisioning rhythms relative to the lunar phase, we examined nest attendance rates and arrival time at the colony for each sex during the new, waning and waxing quarters and full moon. Nightly attendance rates for each sex were Z-transformed to account for the higher average attendance rates of males, which was then compared across sexes and lunar phase through a two-way ANOVA. We assessed arrival time (minutes since sunset) as a function of sex and lunar phase with adult identity as a random effect using a LMM. The significance of each explanatory variable was assessed with the 'Anova' function using type III Wald χ^2 tests from the R package car (Fox and Weisberg 2011).

Chick condition for each day was calculated as the residual of body mass regressed on body size, which was calculated from the factor score of the first principal component of tarsus, head-bill and wing chord (Weimerskirch and Cherel 1998). Since chick morphometric measurements were only

taken every three days, predicted values for each morphometric measurement were used to interpolate between measurements. Predicted values were found by fitting a logistic model to tarsus and head bill and a quadratic model to wing chord using the *easynls* R package (Arnhold 2017). We then used this measure of chick condition to assess whether adults of each sex adjusted meal size relative to chick condition through a LMM with adult identity as a random effect. Furthermore, we assessed how chick condition at a start of a foraging trip affected the duration of the foraging trip for each sex through a separate LMM with adult identity as a random effect. As above, the significance of each explanatory variable was assessed using type III Wald χ^2 tests.

If one sex is energetically constrained from provisioning at higher rate, we would expect to observe greater within-individual variation in trip duration, as occurs in dual-foraging species that alternate between short and long trips for the purpose of chick and self-provisioning, respectively (Chaurand and Weimerskirch 1994). Trip duration variation was calculated for each individual with at least three foraging trips, as this is the minimum number of necessary trips to calculate variation. Given that short foraging trips provide less time for self-provisioning and are thus more energetically demanding, we also explored how individuals responded after making single day trips, the shortest observed trip duration. To do so, we compared the duration of trips after single day trips between males and females with individual as a random effect through a LMM. Additionally, we compared the observed distribution of trip durations after single day trips to the expected distribution for males and females. To generate the expected distribution, we used the overall pool of recorded trip durations, which was then compared to the observed trip duration distribution following single day trips through χ^2 tests for males and females separately.

Results

Provisioning behavior

Hatch dates for RFID monitored burrows ranged between 10 July and 16 August, with a mean hatch date of 26 July. Following hatching, our RFID reader array monitored 2605 chick nights and recorded 221 520 detections from 148 parents (74 pairs). Across all individuals measured in our study colony, morphometric measurements differed by less than 1.6% between the males and females (Table 1). After classifying detection sequences, we identified 1589 foraging trips. We also identified 63 brooding stints, which were excluded from further analysis. Females and males showed distinct foraging behavior with males making significantly shorter duration trips than females (2.1 ± 0.1 days and 2.8 ± 0.1 days, respectively, LM: $p < 0.001$, Fig. 1).

During chick-rearing, we collected 2470 masses from the 74 chicks in RFID monitored burrows. Across all burrows, chicks were unfed on 38% of the monitored nights and fed by either one or two parents on 47% and 15% of nights,

Table 1. Average measurements for wing chord, tarsus and mass of males and females banded between 2014 and 2016 within our study colony. Standard deviations for each measurement are given in parentheses. The percent difference between each measurement is calculated as one minus the smaller measurement divided by the larger measurement.

Measurement	Male (n=180)	Female (n=211)	Difference (%)
Wing chord length (mm)	162.2 (3.4)	164.6 (3.3)	1.4
Tarsus length (mm)	24.4 (0.8)	24.7 (0.8)	1.1
Mass (g)	46.4 (4.3)	47.1 (4.6)	1.6

respectively. The average meal size after a visit by one and two parents was 3.5 ± 4.3 g and 10.7 ± 5.3 g, respectively. The top model of daily mass change included the number of provisioning parents, chick mass and previous trip duration ($R^2 = 0.48$, each fixed effect $p < 0.001$). The next best model ($\Delta AIC = 1.47$) included the same terms as the top model as well as the sex of the provisioning parent, though this term was not significant ($p = 0.35$). Other candidate models had ΔAIC greater than 5 from the top model and so were not considered further (Burnham and Anderson 2004).

Though the sex of the provisioning parent was not related to daily chick mass change, the total mass change across the provisioning period due to males (25.7 ± 0.26 g) was significantly greater than that due to females (18.4 ± 0.17 g, paired t -test $t_{76} = 3.18$, $p = 0.008$).

Tests for sex-specific provisioning

We did not observe differences in nest attendance rates relative to moon phase (ANOVA, $F_{3,54} = 1.752$, $p = 0.167$). This was true for both sexes (ANOVA, $F_{1,54} < 0.001$, $p = 0.99$) and there was no interaction between moon phase and sex (two-way ANOVA, $F_{3,54} = 0.831$, $p = 0.83$). Arrival time at the nest after sunset varied by lunar phase with individuals returning later during the full moon (LMM, $\chi^2 = 44.9$, $p < 0.001$; Tukey test, $p < 0.001$ for all combinations between the full moon and all other phases). There was no general difference in arrival times between sexes (LMM, $\chi^2 = 0.06$, $p = 0.80$) and we found no evidence for an interaction between sex and lunar phase on arrival time (LMM, $\chi^2 = 2.22$, $p = 0.53$).

Both males and females responded to chick condition and increased meal size after encountering a chick in poor condition (LMM, $\chi^2 = 78.1$, $p < 0.001$). We observed an interaction between adult sex and chick condition on the duration of the subsequent foraging trip (LMM, $\chi^2 = 7.69$, $p < 0.001$, Fig. 2) with females increasing foraging trip duration after encountering a chick in good condition, while males did not adjust foraging trip duration.

Females showed greater within-individual variation in trip duration than males (ANOVA, $F_{1,123} = 13.8$, $p < 0.001$). Additionally, after making an energetically taxing, single day trip, females took longer subsequent trips than males (LMM, $\chi^2 = 58.5$, $p < 0.001$). The observed versus expected distributions of trip lengths following one day trips were also significantly different for females ($\chi^2_{(6)} = 46.3$, $p < 0.001$) and

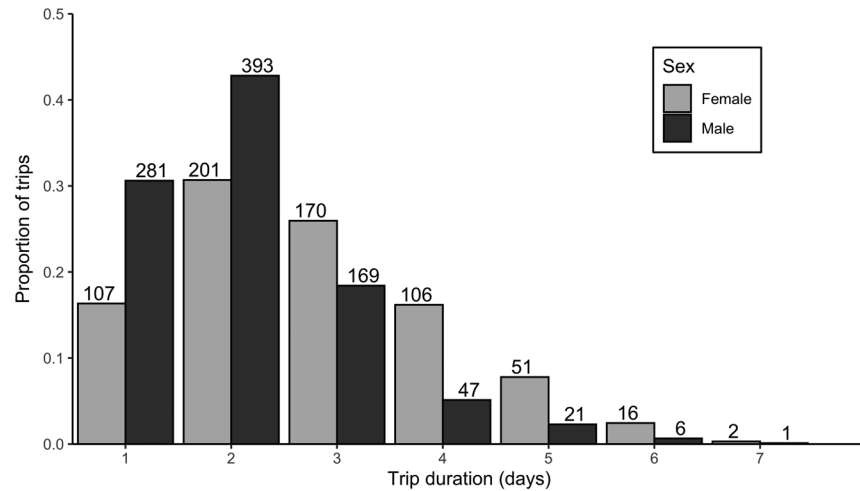


Figure 1. Relative frequencies of trip lengths (in days) for male and female Leach's storm-petrels on Bon Portage Island. Counts of each trip length are given above each bar. In addition to the trips shown, one male made a trip of eight days and two females made trips of nine days.

males ($\chi^2_{(4)} = 34.8$, $p < 0.001$), and this was driven by females making longer trips than would be expected and males following the opposite pattern (Fig. 3).

Impacts of RFID readers and PIT tags

No birds were observed to abandon in response to tagging as all adults returned to the nest at least once after being tagged. In prior years, where we minimally handled adults using the

same regime as described here and chick morphometrics were collected every 5 days, 11% of the chicks that hatched died. In this study, where burrows were outfitted with RFID readers, adults were given PIT tags, and chicks were handled daily, 3% of chicks that hatched in RFID burrows died ($n=2$). Moreover, the average mass of chicks in non-RFID monitored burrows was not significantly different from the average mass of chicks of the same age in RFID-monitored burrows, which suggests that chick growth in RFID-monitored burrows was

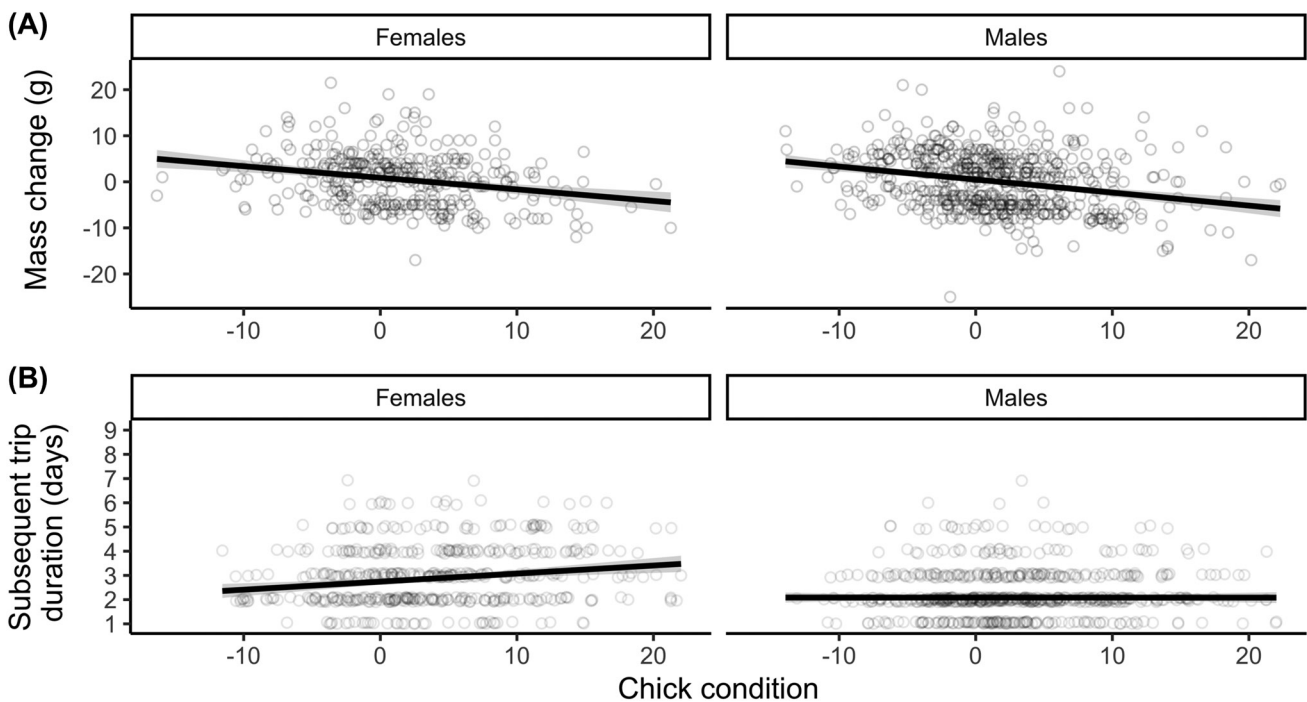


Figure 2. (A) Chick mass change (g) as a function of chick condition for females (left) and males (right). Chick condition was determined based on the residual of the regression of body size (the first factor of a principal components analysis of tarsus, wing chord and head bill) against mass on each day. Smaller numbers indicate a lower mass relative to body size (i.e. poor condition). (B) Trip duration (days) as a function of chick condition (calculated as above) for females (left) and males (right).

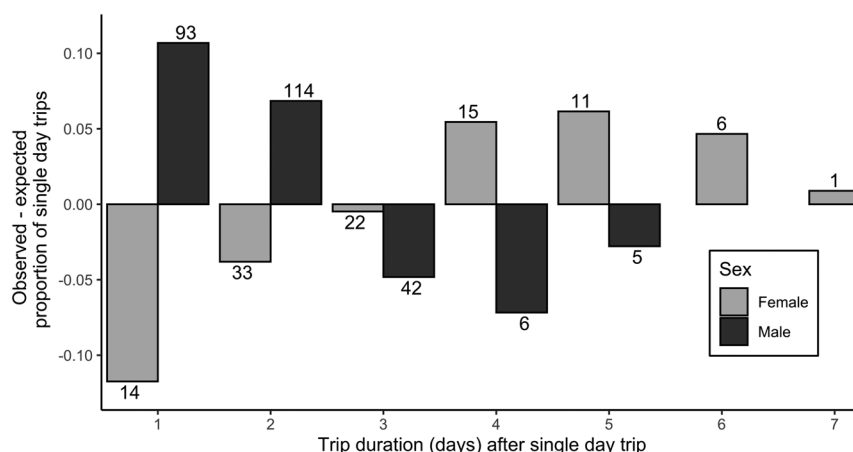


Figure 3. Difference between observed and expected relative proportions of each foraging trip duration following one day foraging trips. Expected values were found by randomly sampling trip durations for each sex. Observed values were based on the actual trip durations made by each sex following a one-day trip.

not adversely impacted (t -test $t_{31} = 1.7$, $p = 0.10$). Based on these findings, there is no indication that the RFID readers and the additional handling of chicks had negative effects compared with our prior sampling protocol.

Discussion

Using data on a large sequence of consecutive foraging trips, we observed distinct sex-specific provisioning behaviors in the sexually monomorphic Leach's storm-petrel across the chick-rearing period. Consistent with previous reports in other populations, the individuals in our study showed negligible size-dimorphism (Crossin 1974, Ainley 1980). Despite being physically similar, males provisioned more frequently and, consequently, provided a greater overall amount of food to their chick. Our findings confirm that male-biased provisioning is likely a general characteristic of this species, rather than being an effect of location or year. Additionally, we examined multiple hypotheses to account for sex-specific provisioning in monomorphic seabirds and found that the energetic constraints hypothesis best explained the reduced provisioning rates of female Leach's storm-petrels.

We did not find support for two of the three hypotheses that have been proposed as explanations of sex-specific provisioning in monomorphic birds. Different nest attendance rhythms did not explain lower provisioning rates by females. Both sexes exhibited similar arrival time and activity at the colony relative to lunar phase. As such, one sex was not consistently encountering a hungrier chick, which could lead them to provision a greater amount or perceive chick condition differently than the other sex. Additionally, sexes showed similar responses to lunar phase, with both males and females returning later during the brighter, full moon suggesting that both sexes are equally cautious about increased predation risk. There is also little support for subtle physical differences between sexes giving rise to the observed differences in provisioning rates, though this was not a mechanism we could

directly test with our data. Leach's storm-petrels are largely solitary at sea with limited interactions during foraging (Pollet et al. 2019), making it unlikely that interference competition results in niche segregation as is observed in other species that congregate at sea (Peck and Congdon 2006). Moreover, as surface-feeding birds, the slight asymmetries in body size are unlikely to give rise to meaningful discrepancies in foraging efficiency such as those observed in diving species where slight differences in mass can profoundly affect diving depth (Lewis et al. 2002, Peck and Congdon 2006).

We found partial support for sex-specific responses to chick condition. Previous studies on provisioning behavior in response to chick condition in Leach's storm-petrels were conducted on individuals of unknown sex and so could not demonstrate an effect of parent sex on provisioning behavior (Ricklefs 1990, 1992, Takahashi et al. 1999). We observed that while both sexes delivered larger meals to chicks in poor condition, only females increased the duration of their subsequent foraging trip after encountering chicks in good condition. This suggests that both sexes are responsive to chick condition, but that females are more likely than males to decrease parental effort when possible. While we measured provisioning effort in terms of daily change in chick mass, it is possible that males and females may deliver meals with differing levels of nutritional quality. Many species adjust provisioning effort in response to chick condition (Weimerskirch et al. 2000, Phillips and Croxall 2003) and in some cases this behavior is sex-specific (Quillfeldt et al. 2004, Low et al. 2012, Ryser et al. 2016). One proposed explanation for sex-specific provisioning rules is that if one sex is energetically constrained it will be selected to more finely regulate levels of parental care (Kilner 2002, Quillfeldt et al. 2008). As such, this finding is also consistent with the final hypothesis we considered.

Overall, our findings provide the most support for the energetic constraints hypothesis. We found that within-individual variation in trip duration was larger for females than males, suggesting that females are alternating between short

and long trips to a greater degree. This pattern is similar to the dual-foraging strategy employed by several other seabird species, which allows individuals to balance self and chick care (Chaurand and Weimerskirch 1994, Weimerskirch et al. 1994). Short duration trips ensure continual provisioning to the chick, but entail a high cost of repeatedly commuting to foraging areas, whereas long duration trips allow individuals to spend more time foraging at the expense of reduced provisioning frequency. Additional support for females being energetically constrained is that after making single day trips, females, unlike males, significantly increased the duration of their subsequent trip, suggesting a need to recover from these short, energetically taxing trips. The observed change in foraging trip duration following single day trips cannot be explained by sex-specific provisioning rules as there was no relationship between single day trips and chick condition (i.e. chicks did not tend to be in better condition after females returned from a single day trip).

As a long-lived species, Leach's storm-petrel typically maximize lifetime reproductive output by prioritizing their own survival over that of their offspring (Williams 1966, Stearns 1977). As such, individuals are not expected to over-invest in parental care at the expense of their own condition. Leach's storm-petrel eggs are exceptionally large relative to adult body size, up to 22% (Montevecchi et al. 1983) and thus represent a substantial initial energetic investment by the female. During egg production, females also pay an energetic cost of higher basal metabolic rates (Whittow 2002). These costs are likely not trivial; in the similarly sized European storm-petrel, after the first breeding season, overwinter survival is significantly lower for females, but not for males (Sanz-Aguilar et al. 2012). Our findings suggest that the large initial investment in the egg places an energetic constraint on females that is apparent during the chick-rearing period, limiting female provisioning.

If breeding is more energetically demanding for females, this may result in female-biased mortality, which could have important population-level effects. A male-skewed adult sex ratio (ASR) is characteristic of many avian species, which is expected to be the result of higher mortality in the rarer sex as most avian species have an even primary sex ratio (Donald 2007). A variety of explanations may account for sex-specific mortality rates, but, in general, reproductive effort is expected to impact female mortality (Székely et al. 2014). Size-relative clutch mass, in particular, is strongly related to female mortality (Sibly et al. 2012). As such, despite male-biased parental effort observed during incubation (Mauck et al. 2011) and chick-rearing (this study and Mauck et al. 2011), female mortality may nevertheless be elevated due to the extreme investment in offspring production, resulting in a male-skewed ASR.

In monogamous species, uneven ASRs, especially if male-biased, are expected to increase a species' extinction risk (Donald 2007). Marine birds, which are almost exclusively monogamous (Cockburn 2006), are one of the most threatened groups of birds (Crocoll et al. 2012). Leach's storm-petrels, though abundant throughout the north Pacific and

Atlantic, are declining locally at several important breeding colonies (Pollet and Shutler 2018, Wilhelm et al. 2020) and their conservation status is considered vulnerable (BirdLife International 2022). Like other long-lived species, adult survival is a key demographic parameter in the population viability of Leach's storm-petrel (Hamer et al. 2001). Our findings suggest that females may be especially sensitive to environmental changes that impact breeding effort. Further research, however, is required to assess how the energetic constraints experienced by breeding females may carry over to future breeding attempts or influence female mortality, which are both processes that may have important population-level effects.

Acknowledgements – We thank Lee and Carlene Adams, Jason Nickerson, Jimmy Kaufmann, Dave Shutler, Phil Taylor and Joshua Hincks for logistical support and assistance at the field site on Bon Portage Island. We also acknowledge Gabrielle Nevitt for her work establishing the study colony on Bon Portage. Further, we thank Eli Bridge and Marcel Losekoot for their assistance in designing the RFID readers used in this study and Hayato Kawaguchi for help constructing the RFID readers. Lastly, we are very grateful to the Hull lab at UC Davis for providing helpful feedback on earlier versions of this manuscript.

Funding – This research was supported by funding from the Henry A. Jastro Research Award through the University of California, Davis, an Explorers Club Grant, and by NSF IOS 1258828.

Permits – Sampling was conducted under the approval of the University of California, Davis Institutional Animal Care and Use Committee Protocol 19288, Canadian Wildlife Service (CWS) Banding permit 10695 and CWS Research permit SC2742.

Author contributions

Chris W. Tyson: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Sarah L. Jennings:** Data curation (supporting); Investigation (supporting); Project administration (lead); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Brian A. Hoover:** Data curation (supporting); Investigation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Amy Miles:** Data curation (supporting); Investigation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Transparent Peer Review

The peer review history for this article is available at <<https://publons.com/publon/10.1111/jav.02904>>.

Data availability statement

Data are available from the Dryad Digital Repository: <<https://datadryad.org/stash/share/E7QsmUjkItfhUIGJwen4u6ANrfZIwySpgna8oSBe6JA>> (Tyson et al. 2022).

Supporting information

The supporting information associated with this article is available from the online version.

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