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Migratory life histories explain the extreme egg-size dimorphism of *Eudyptes* penguins

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When successive stages in the life history of an animal directly overlap, physiological conflicts can arise resulting in carryover effects from one stage to another. The extreme egg-size dimorphism (ESD) of *Eudyptes* penguins, where the first-laid A-egg is approximately 18–57% smaller than the second-laid B-egg, has interested researchers for decades. Recent studies have linked variation in this trait to a carryover effect of migration that limits the physiology of yolk production and egg sizes. We assembled data on ESD and estimates of migration–reproduction overlap in penguin species and use phylogenetic methods to test the idea that migration–reproduction overlap explains variation in ESD. We show that migration overlap is generally restricted to *Eudyptes* relative to non-*Eudyptes* penguins, and that this overlap (defined as the amount of time that egg production occurs on land versus at sea during homeward migration) is significantly and positively correlated with the degree of ESD in *Eudyptes*. In the non-*Eudyptes* species, however, ESD was unrelated to migration overlap as these species mostly produce their clutches on land. Our results support the recent hypothesis that extreme ESD of *Eudyptes* penguins evolved, in part, as a response to selection for a pelagic overwinter migration behaviour. This resulted in a temporal overlap with, and thus a constraint on, the physiology of follicle development, leading to smaller A-egg size and greater ESD.

1. Introduction

Traditionally, it was assumed that life-history stages such as migration, breeding and moult were organized so that direct overlaps between activities were minimized [1]. However, it has become increasingly clear that successive life-history stages can directly overlap [2], as can the underlying physiologies, resulting in carryover effects from one stage to another [3]. Such carryover effects can be mediated by resource partitioning, or by physiological or hormonal 'conflicts' between the regulatory systems of different life-history processes when they operate simultaneously (e.g. locomotion versus reproduction) [2,4]. Depending on context, these conflicts can have positive, negative or neutral effects on fitness [2]. For example, environmental conditions during the non-breeding stage of the annual cycle can influence decisions about migratory and foraging behaviours, which can then influence an individual's relative condition and physiological readiness for reproduction weeks or even months later [5,6]. In birds, males of some migratory species are known to initiate reproductive development long before their arrival at breeding areas. In the trans-equatorial garden warbler (*Sylvia borin*), for example, males begin secreting testosterone and developing their testes late in migration while on the wing [7]. Similarly, in American redstarts (*Setophaga ruticilla*), male arrival date at breeding grounds is positively correlated with testosterone levels [8]. Although this did not result in advanced readiness for reproduction in the redstarts, testosterone had positive pleiotropic effects on their migratory behaviour such that birds with high levels arrived early [8]. For female birds, there is limited evidence that

reproductive development is also initiated during migrations [2], with examples mostly in the penguins [9–11]. In some species, egg production (e.g. vitellogenesis, follicle development) can begin when females are migrating back to breeding colonies, and in the highly migratory crested penguins (*Eudyptes* spp.), migratory activity has been linked to a unique reproductive pattern of extreme egg-size dimorphism (ESD) [9–13].

The functional and evolutionary significance of the extreme ESD of *Eudyptes* penguins has interested researchers for decades [14], and was highlighted by David Lack and V. C. Wynne-Edwards in their early debates about clutch size evolution and group selection. The penguins are a small avian family of 18 species (Spheniscidae), which exhibit pronounced variation in reproductive life history [11], and most species have a clutch size of two, the exceptions being the single-egg emperor penguins *Aptenodytes forsteri* and king penguins *A. patagonicus*. Among the two-egg species, those within the genus *Eudyptes* exhibit an extreme degree of ESD, where the first-laid A-egg is 18–57% smaller than the second-laid B-egg [11,12]. This is coupled with obligate brood size reduction directed at the smaller A-egg; in almost all cases, the surviving chick is hatched from the B-egg [15,16]. Such extreme ESD is unmatched in any other bird species and may represent a rare example of an evolutionary transition towards a single-egg clutch [13,14]. *Eudyptes* also differ from other two-egg penguins by embarking on pelagic overwinter migrations, with individuals ranging over approximately 2 million km² throughout the southern latitudes during the approximately six-month non-breeding period [17,18], and then making rapid return migrations back to breeding colonies [17]. Female *Eudyptes* penguins initiate egg production during these return migrations [9,10], and in macaroni penguins (*E. chrysolophus*) and rockhopper penguins (*E. chrysocome*), ESD is inversely correlated with time between arrival at the breeding ground and egg laying [10,19]. The latest-arriving females generally produce the most dimorphic eggs and have lower plasma levels of the yolk precursor vitellogenin; that is, they show lower reproductive 'readiness' upon arrival [10,19]. Although other factors can contribute to variation in ESD (see [20] and Discussion), these studies support the hypothesis that variation in extreme ESD in *Eudyptes* penguins is partially owing to a physiological constraint imposed by migratory activity [9,10,13]. However, this idea has not yet been tested across the Spheniscidae, within a phylogenetic framework.

Here, we assemble published data on ESD for the 16 penguin species possessing two-egg clutches. We then use phylogenetically controlled models to explore variation in ESD relative to an index of the overlap between migratory activity and reproductive development, which we specifically define as the time interval between arrival at the breeding colony and the initiation of laying [9]. The development of immature ovarian follicles to mature egg yolks (i.e. rapid yolk development time, RYD) takes approximately 15 days in the two-egg penguins (range 14–17 days [21]. We therefore assume that a migration–reproduction overlap will be highly correlated with ESD, but only when the laying interval is less than RYD. In other words, if the time between arrival and laying is less than RYD, then ESD should be evident as follicle development would have been initiated prior to colony arrival during migration. If the arrival to laying interval is more than RYD, then ESD should be minimal or zero. This result would provide support for the hypothesis that extreme ESD in *Eudyptes* has evolved, in part, from selection for

pelagic migration behaviour [13] and an associated constraint on follicle development, perhaps via the physiology of yolk production [9,10,19].

2. Material and methods

From the scientific literature, we assembled data on female pre-laying body mass, A- and B-egg masses, ESD and an index of migratory overlap. The *Aptenodytes* penguins (e.g. king penguins and emperor penguins) were excluded from the analysis simply because they produce a single-egg clutch, and so ESD does not occur. ESD was calculated as the ratio of A-egg to B-egg mass. Migratory overlap was calculated as the interval in days between arrival of the female in the breeding colony and laying date [9]. Table 1 summarizes these data, and an annotated table of overlap estimates with citations to published sources can be found in the electronic supplementary material (table S1). All data were critically assessed to provide best-known estimates for each variable (see Discussion). Figure 1 shows the phylogeny of all two-egg species in the Spheniscadae, and tabulates their migratory or non-migratory (i.e. resident) tendencies [22,23] (we have included *Aptenodytes* for illustrative purposes only, to indicate their position within the family). Theoretically, it is difficult to define the 'arrival' dates of females of non-migratory species, and therefore difficult to calculate their pre-laying intervals (e.g. females may be in or near the colony everyday before laying). Although some published estimates are available (see electronic supplementary material, table S1), we fixed the interval for the only resident species for which we could not find published estimates (e.g. Galapagos, black-footed and white-flippered penguins; electronic supplementary material, table S1) at 15 days, which is the mean of RYD times for penguins and the presumed minimum time interval before laying for resident species (see Discussion).

We used phylogenetic generalized least-squares (PGLS) regression analysis to explore the relationship between migratory overlap and ESD, while controlling for allometric effects related to female arrival body mass. Pagel's λ provides a maximum-likelihood estimate of phylogenetic autocorrelation or signal. The evolution of species traits is independent of phylogeny when $\lambda = 0$. The importance of phylogeny increases when $\lambda > 0$, and conforms to Brownian motion when $\lambda = 1$. The value of λ is a scaling factor for a correlation, and not a correlation coefficient itself, so a λ slightly greater than 1.0 is theoretically possible [24]. Our model incorporated a published molecular phylogeny for the Spheniscidae [22] (figure 1). Species were categorized as either *Eudyptes* or non-*Eudyptes* (class variable). α was set at 0.05. Analysis was run using the APE package in R [25].

3. Results

ESD differed significantly between *Eudyptes* and *non-Eudyptes* (figure 1; $t_{10} = 11.760$, $p < 0.0001$). Consistent with our prediction, this ESD was significantly correlated with the index of migratory overlap, but only in the *Eudyptes* penguins and not in non-*Eudyptes* penguins (figure 2; $\lambda = 1.02$, $n = 16$, class $t_{10} = 2.252$, $p = 0.044$, interval $t_{10} = 5.819$, $p = 0.0002$, class × interval $t_{10} = -5.522$, $p = 0.0003$). Female pre-laying body mass had no significant effect in the model ($p = 0.394$), nor did its interaction with the class variable (*Eudyptes* or non-*Eudyptes*; $p = 0.415$). When the model is re-run without the three species for which we do not have published interval estimates (open circles in figure 2; table 1), the significance levels and parameter estimates do not change meaningfully
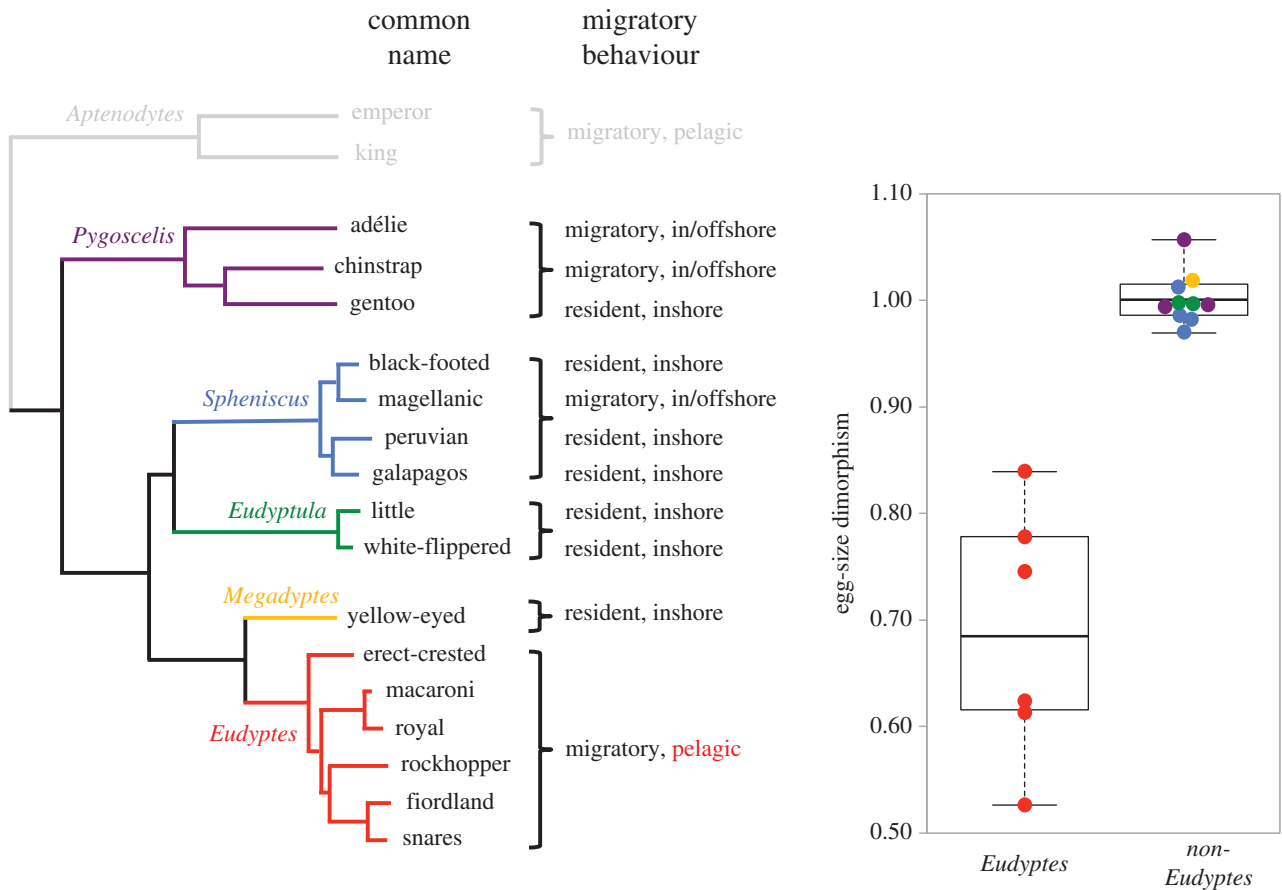
Figure 1. Molecular phylogeny of the 16 two-egg penguin species with Bayesian posterior support probabilities (data from [22]), and indication of non-breeding foraging tendencies [23]. The genus *Aptenodytes* was not included in the analysis as these penguins produce only a single-egg clutch, but they are presented to indicate their position in the Spheniscadae. Also shown is a boxplot comparing the extent of egg-size dimorphism in *Eudyptes* and *non-Eudyptes*. Points in the boxplot are colour-coded to genus.

Table 1. Biological characteristics of the two-egg-clutch penguin species used in the comparative analysis of egg-size dimorphism. The penguin genus *Aptenodytes* is not included as its species produce only a single-egg clutch. Comments on interval data are provided in the electronic supplementary material, table S1.

common name	scientific name	A-egg mass (g)	B-egg mass (g)	ESD	arrival to laying interval (d)
Adélie	*Pygoscelis adeliae*	122.8	115.3	1.065	17.0
chinstrap	*Pygoscelis antarcticus*	102.2	102.5	0.997	17.4
gentoo	*Pygoscelis papua*	128.2	120.0	1.013	25.0
black-footed	*Spheniscus demersus*	106.8	104.8	1.019	25.0
Magellanic	*Spheniscus magellanicus*	124.9	124.7	1.002	15.0[b]
Peruvian	*Spheniscus humboldti*	121.2	125.1	0.969	31.0
Galapagos	*Spheniscus mendiculus*	79.6	80.9	0.984	15.0[b]
little	*Eudyptula minor*	53.7	53.5	1.004	21.0
white-flippered	*E. minor albosignata*	60.0	59.7	1.005	15.0[b]
yellow-eyed	*Megadyptes antipodes*	139.4	136.9	1.018	30.0
erect-crested	*Eudyptes sclateri*	81.6	150.9	0.541	10.5
macaroni	*Eudyptes chrysolophus*	92.7	149.4	0.620	10.5
royal	*Eudyptes schlegeli*	100.3	159.3	0.630	10.0
rockhopper[a]	*Eudyptes moseleyi*	84.5	113.2	0.746	14.0
Fiordland	*Eudyptes pachyrhynchus*	99.4	118.5	0.839	15.0
Snares	*Eudyptes robustus*	103.3	132.5	0.780	13.5

[a]The rockhopper penguins were recently divided into northern (*E. moseleyi*), southern (*E. chrysocome*) and eastern (*E. filholi*) species.
[b]Interval estimates are not available (see electronic supplementary material, table S1), and so are fixed at a mean RYD time of 15 days (see Material and methods).

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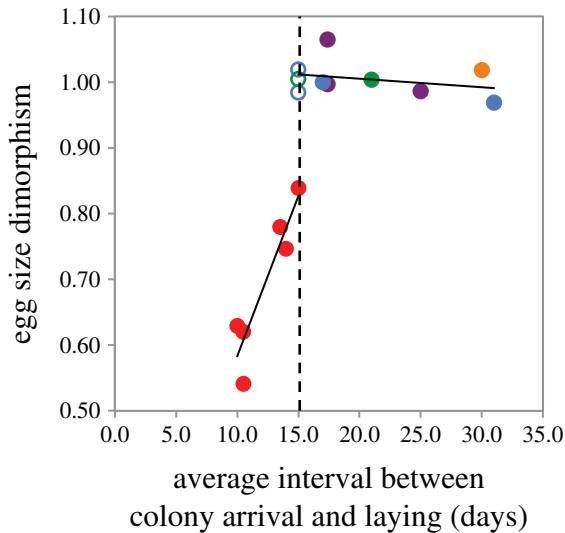
Figure 2. Phylogenetic generalized least-squares regression model showing the relationship between egg-size dimorphism and migration–reproduction overlap, defined here as the time interval on land between colony arrival and the initiation of egg laying. Egg-size dimorphism is positively correlated with interval in *Eudyptes* penguins (red points) but not in the non-*Eudyptes* (all other colours as identified to genus in figure 1). The open points (colourless centres) indicate the resident species for whom pre-laying interval on land was fixed at 15 days, which is the mean duration of rapid yolk development times (dashed line; see Material and methods, and table 1). As predicted, extreme ESD occurs when the interval between arrival and laying is less than RYD time, which suggests that follicle development began at sea. Note that the 15-day RYD line is the mean RYD value calculated for three species (see Discussion); the mean value calculated for *Eudyptes* only is 16 days, whereas for little penguins and Adélie penguins, it is 14 and 15 days, respectively.

(e.g. the results and interpretation are the same with and without these three species).

4. Discussion

We tested the hypothesis that the extreme ESD of *Eudyptes* penguins evolved, in part, via selection for pelagic, overwinter migration behaviour, which results in a temporal overlap and thus a trade-off with the physiology of follicle development [13]. Our results clearly show that migration–reproduction overlap (arrival-to-laying interval less than RYD) is characteristic of the genus *Eudyptes*, and that the extent of overlap strongly predicts the magnitude of ESD (figure 2). In contrast, the other four two-egg penguin genera (*Pygoscelis*, *Spheniscus*, *Megadyptes* and *Eudyptula*) exhibit no discernible overlap between migration and egg production (laying interval more than RYD), and both eggs of their clutches are consequently the same size (ESD ∼ 1). The relationship between migration–reproduction overlap and ESD in *Eudyptes* was not an artefact of phylogenetic autocorrelation, as our models controlled for phylogeny, nor was it influenced by female pre-laying body mass. Our study therefore strongly suggests that the difference between *Eudyptes* and non-*Eudyptes* in terms of ESD lies in how the duration of migration–reproduction overlap relates to that of rapid yolk development, which is itself a product of their evolutionary history.

Before we discuss how migratory overlap relates to RYD, we will put our main results into a broader context. We show

that the difference between migration–reproduction overlap and egg sizes in *Eudyptes* and non-*Eudyptes* penguins is striking (figure 2), but as with any comparative analysis we acknowledge that confidence in the quality of available data is paramount. We critically evaluated the published literature citing arrival-to-laying intervals/overlap and ESD, and summarize these in the electronic supplementary material, table S1 and in table 1, but discuss this further here. In our review of the literature, the only anomaly that we identified in overlap estimates was for the Adélie penguins (*Pygoscelis adeliae*). The literature on Adélie penguins shows that ESD is well established at approximately 1.065, and the majority of sources suggest that this species has a long pre-laying period on land, averaging 21 days [26], and as high as 28 days at some colonies. This is much greater than their RYD period of approximately 15 days (see electronic supplementary material, table S1). However, for at least one population, a pre-laying period as low as 10 days has been reported [27]. Despite the possibility for a migration–reproduction overlap in Adélie in rare cases (electronic supplementary material, table S1), via a short arrival-to-laying interval, Adélie are essentially inshore foragers, dispersing sometimes great distances from breeding colonies during winter, but usually within continental margins and the sea-ice edge [28]. Although some Adélie and several other non-*Eudyptes* species can travel distances similar to or even greater than *Eudyptes* during the non-breeding period [28–30], it is not the total distance travelled, but the speed of the return migration that distinguishes *Eudyptes* spp. from other penguins. During their return to colonies, *Eudyptes* swim at nearly twice the speed of non-*Eudyptes* (e.g. approximately 72 km day^{-1} in rockhoppers [31] versus approximately 32 km day^{-1} in Adélie [28]; travel speeds are generally well documented in *Eudyptes* [17] but less so in other species), which is perhaps characteristic of pelagic over-winter migration behaviour [13]. The expeditiousness of these return migrations may be the key characteristic of *Eudyptes* that creates a physiological conflict between migratory activity and follicle development, leading to their extreme ESD [10]. In contrast, Adélie penguins tend to forage in near-shore polynyas and ice edges close to breeding colonies in the days to weeks preceding arrival at breeding colonies [32]. In cases where their arrival-to-laying interval is shorter than RYD times of approximately 15 days (electronic supplementary material, table S1), portions of this time can also be spent 'tobogganing' over sea ice rather than actively swimming (e.g. sliding on their bellies, which is energetically less expensive than either swimming or walking [33]). For these reasons, we suggest that the physiological and energetic demands exacted from Adélie penguins during their slower, in-shore return migrations must be very different from the demands of expeditious migrations typical of *Eudyptes*, and may explain why in the rare cases where pre-laying intervals of Adélie are shorter than RYD times, ESD is still approximately 1.

What is the mechanism underpinning, and the consequence of, the overlap between migratory activity and rapid yolk development in penguins? As mentioned previously, RYD is an essential component of egg production that leads to the development of a mature yolky follicle, the relative size of which influences albumen secretion and final egg size [2,34]. As we show, there is a strikingly different relationship between migration overlap and RYD in *Eudyptes* versus non-*Eudyptes* penguins. RYD lasts approximately 16 days in *Eudyptes* (*E. pachyrhynchus*), and approximately 14 and 15 days in the

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other two penguin species for which this has been quantified (*Eudyptula minor* and *Pygoscelis adeliae*, respectively [21]). What our analysis suggests is that when the interval between arrival and egg laying is less than the predicted RYD time, there is an apparent overlap between the demands of migratory activity (e.g. swimming) and the physiology driving yolk production. Because the development of the first yolky follicle, which gives rise to the first egg of the clutch (i.e. the A-egg), precedes that of the second follicle by around 4 days [27,35], any physiological conflicts or constraints arising between migration and follicle development should disproportionately affect the A-egg [9,10] (coupled with the exponential pattern of follicle growth any direct effect of overlap on B-egg size will be small). Within *Eudyptes*, there is a linear relationship between interval and ESD such that short intervals (which equals greater migration–reproduction overlap) yield highly dimorphic eggs, whereas longer intervals yield less dimorphic eggs. However, when the interval exceeds that of the predicted RYD, as is the case for all other non-*Eudyptes* species, egg production occurs entirely on land and free from migratory constraint, and there is essentially no dimorphism between eggs (ESD ∼ 1). We can only speculate as to the physiological mechanism responsible for limiting follicle development that underlies ESD [10,19], but HPA upregulation of glucocorticoid hormone secretion to sustain active metabolism and locomotor activity [36–38] may exert anti-gonadotropic effects, which has been previously documented in birds and linked to reductions in yolk precursor levels and egg sizes [39].

Our results clearly support the hypothesis that a migration–reproduction overlap can constrain egg production in *Eudyptes* penguins, where greater overlap disproportionately affects the A-egg, leading to smaller A-egg size and greater ESD [9,10]. Although the specific mechanism has not been identified, we view this as a classic 'trade-off', but one that might involve a physiological conflict [4] rather than involve simple resource partitioning. As the impact of this migratory conflict or trade-off has an effect on the ensuing pattern of reproductive investment at the time of egg laying (and subsequently in terms of realized fecundity [13]), we think this also fits the definition of a 'carry-over' effect [3]. Thus, one of the most intriguing questions is why the consequences of this constraint have persisted in *Eudyptes* penguins, and why they have retained a two-egg clutch despite millions of years of evolution (this maladaptation is dealt with at length in [13]). In birds, there is a widespread fitness advantage associated with early onset of egg laying [2], which suggests that there is strong selection for early onset of reproductive development in penguins, especially at higher latitudes [13]. However, it is this coupled with the evolution of a slowed life history and, specifically, pelagic overwinter migration behaviour [13] that explains ESD in *Eudyptes* penguins alone. Therefore,

migration–reproduction overlap leads to a direct constraint on follicle development, reducing A-egg size and generating variation in ESD across the *Eudyptes* clade.

We acknowledge that other factors have probably contributed to the evolution of ESD. For example, there is most certainly a genetic component to ESD, as female *Eudyptes* breeding in captivity still produce dimorphic eggs, despite ample food supply, and lack of any migratory demands, although the extent of ESD tends to be less that that observed in the wild [40]. Individual repeatability in ESD has also been reported, at least for one species (rockhoppers), although there remains a high degree of interindividual variation [20]. Finally, recent work has shown that B-egg allometry is positive and uniform across two-egg-clutch Spheniscidae (despite differences in migratory overlap and ESD) but that ESD in *Eudyptes* is associated with a 5.4% increase in relative B-egg size [13]. Larger B-egg size could certainly be viewed as an adaptive response to a maladaptive situation (i.e. compensation for the migratory constraint imposed on A-egg development). This suggests that B-egg size might be optimized to enhance survival in a one-chick brood [13], though there is currently no evidence that variation in B-egg size affects offspring growth or survival [9]. Nevertheless, our comparative analysis of ESD suggests that a migratory constraint on follicle development, perhaps through effects on yolk precursor production [10], is the key mechanism contributing to the evolution of extreme ESD in *Eudyptes* penguins. ESD can therefore be considered a hallmark of clutch-size maladaptation, resulting from a slowed life history and selection for pelagic overwinter migrations [13]. Future comparative studies that examine relationships between migration overlap and individual A- and B-egg/yolk formation times might reveal different selection pressures that affect the relative size of each egg. Data on individual egg formation times however are presently limited in penguins [21]. More precise monitoring of penguin colonies and overwinter tracking efforts would also provide better estimates of arrival-to-laying intervals for some species, and further elucidate this evolutionary enigma.

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