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Extreme Intraclutch Egg-Size Dimorphism in *Eudyptes* Penguins, an Evolutionary Response to Clutch-Size Maladaptation

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ABSTRACT: *Eudyptes* penguins (six species) are uniquely characterized by a two-egg clutch with extreme intraclutch egg-size dimorphism (ESD): the first-laid A-egg is 17.5%–56.9% smaller than the B-egg. Although A-eggs are viable, they almost never produce fledged chicks (genus average <1%). Using classical life-history theory and phylogenetic comparative methods, we demonstrate a marked slowdown in the life history of *Eudyptes*: age of first reproduction is 52% later and annual fecundity 48% lower compared with other two-egg clutch penguin species. All six *Eudyptes* species have retained a two-egg clutch, despite this pronounced life-history slowdown; this suggests evolutionary mismatch between clutch size and chicks fledged per clutch. Consistent with this, we show that *Eudyptes* fledge 43% fewer chicks per clutch than other two-egg clutch penguin species. Extreme intraclutch ESD in *Eudyptes* is associated primarily with a uniform (5%) increase in relative B-egg size, and B-egg size has evolved in accord with life history. We further show that intraclutch ESD is positively correlated with age of first reproduction in *Eudyptes* but not in other two-egg clutch penguin species. We argue that *Eudyptes*' persistent failure to evolve a one-egg clutch constitutes a unique genus-wide evolutionary maladaptation and that extreme intraclutch ESD evolved as a correlated response to selection favoring a slower life history imposed by their extreme pelagic overwintering and migration ecology.

Keywords: *Eudyptes*, intraclutch egg-size dimorphism, life-history evolution, maladaptation, selective constraint, Spheniscidae.

Introduction

Life histories encompass the major demographic traits associated with fitness and describe variation in schedules for growth, survival, and reproduction (Stearns 1992). Life-history trajectories evolve in response to age-specific mortality schedules but are constrained by trade-offs and evolutionary history (Stearns 1992; Charlesworth 1994;

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Roff 2002). Classical life-history theory assumes that traits with clear, direct links to fitness, such as clutch size, are optimized by natural selection (Charlesworth 1994; Roff 2002). However, a lack of standing phenotypic variation (e.g., most pelagic seabird species have small, invariant clutch sizes of one or two eggs; Hamer et al. 2002) could impede trait optimization (Crespi 2000). Evolutionary stasis, including clutch-size invariance in pelagic seabirds, has been explained by persistent stabilizing selection leading to constraints mediated by selection (Stearns 1986). Selective constraints are considered weak forms of evolutionary constraint because constraint is enforced by selection, not by the nonrandom production of variants (Schwenk 1995). Constraints maintained by relatively weak stabilizing selection relax when selection pressures shift; however, strong and persistent selection can lead to trait canalization (Charlesworth et al. 1982; Stearns 1986). If the clutch-size invariance typical of pelagic seabirds resulted from canalization, then this could constrain clutch-size evolution and lead to maladaptation (Crespi 2000).

Pelagic seabirds have slow life histories (small invariant clutch sizes, low annual fecundity, and deferred reproduction) that are shaped, in part, by the large incremental costs associated with provisioning chicks (Weimerskirch 2002). This cost of reproduction can limit annual fecundity by negatively impacting adult survival and by exerting strong, persistent stabilizing selection on clutch size (Weimerskirch 2002). Penguins (Spheniscidae) have the slow life histories typical of pelagic seabirds, even though most penguin species are inshore forgers (Williams 1995). Part of the reason for this is that penguins are flightless, and flipper-propelled swimming is an expensive means of transport. Despite these higher relative transportation costs, *Eudyptes* penguins (six species) evolved novel pelagic overwintering behavior that involves a temporally and energetically demanding prebreeding migration (Bost et al. 2009; Green et al. 2009). *Eudyptes* penguins are further

characterized by a form of intraclutch egg-size dimorphism (ESD) that is unique (first-laid A-egg is smaller) and extreme (range, 17.5%–56.9%) among birds (Slagsvold et al. 1984; Williams 1995). In *Eudyptes*, extreme intraclutch ESD is coupled with systematic loss of the A-egg, which is viable (Williams 1990; Davis and Renner 2003; Poisbleau et al. 2008) but almost always fails to produce a fledged chick (genus average <1%; Williams 1995). Early, systematic loss of A-eggs or A-chicks is assured by obligate clutch and brood reduction tactics that favor B-eggs (St. Clair 1992, 1996; St. Clair et al. 1995). In *Eudyptes schlegeli* (royal penguin), A-eggs are lost at or before the time B-eggs are laid; this systematic, early loss of A-eggs has been attributed to maternal egg ejection and interpreted as maternal infanticide (St. Clair et al. 1995). *Eudyptes* penguins appear to sacrifice the time and energy invested in A-egg production, and this suggests that their two-egg clutch is maladaptive.

Extreme intraclutch ESD in *Eudyptes* has defied explanation, despite more than 50 years of research (Lack 1968; Johnson et al. 1987; Williams 1990; St. Clair 1992, 1998; St. Clair et al. 1995). The many hypotheses advanced in explanation have focused on adaptive functions for the smaller A-egg; however, the primary candidate hypotheses—brood reduction (Lack 1954) and insurance against B-egg loss (Dorward 1962)—have not received empirical support (Slagsvold et al. 1984; St. Clair et al. 1995). These hypotheses emphasize intraclutch ESD, not clutch size. Alternatively, we propose that extreme intraclutch ESD evolved as a correlated response to selection favoring a slower life history imposed by *Eudyptes*' unique pelagic overwintering and migration ecology. If life history has slowed down in *Eudyptes*, then we would expect clutch size to decrease from two eggs to one egg, as seen in *Aptenodytes* penguins (Williams 1995). However, all six species in *Eudyptes* have retained a two-egg clutch. Here, we use classical life-history theory and phylogenetic comparative methods to demonstrate that life history has slowed down in *Eudyptes* and their two-egg clutch is maladaptive. Retention of a two-egg clutch despite a slowdown in life history suggests that there might be an evolutionary mismatch between clutch size and realized fecundity (number of chicks fledged per two-egg clutch) in *Eudyptes*. If clutch size has become stuck at two eggs in *Eudyptes*, this raises a question: how should egg size evolve when clutch size is fixed and life history slows down? We use allometry to determine whether extreme ESD in *Eudyptes* is the result of a relative decrease in A-egg size, a relative increase in B-egg size, or a combination of the two. Selection favoring a slower life history in combination with a fixed two-egg clutch raises the possibility that extreme intraclutch ESD in *Eudyptes* resulted from an interaction between these processes; consistent with this, we show that

intraclutch ESD is correlated with deferred onset of reproduction (mean age of first reproduction) in *Eudyptes* but not in other two-egg clutch penguin species.

Our analysis provides support for the interpretation that *Eudyptes*' two-egg clutch is maladaptive (sensu Crespi 2000). This raises a second question: what might be precluding clutch-size optimization? Constraint-based explanations are subject to criticism because it is always possible to postulate a rare selective regime where a putatively maladaptive trait could be adaptive (Schwenk 1995). For example, it is plausible that an invariant two-egg clutch coupled with extreme intraclutch ESD could be advantageous during infrequent periods of superabundant resources associated with a long-term (decadal or greater) environmental cycle. Acknowledging this possibility, we suggest that constraint on clutch-size reduction might be related to an interaction between the physiology of follicle (yolk) development and *Eudyptes*' unique pelagic nonbreeding and migration ecology (see "Discussion").

Material and Methods

The Spheniscidae includes the six genera and 18 species of extant penguins (Baker et al. 2006; fig. 1), which exhibit substantial variation in body mass and life-history characteristics (1–24 kg; Williams 1995). The two largest species (*Aptenodytes*; 10–24 kg) first reproduce at 5–6 years, do so once a year or once every other year, and have a one-egg clutch (Williams 1995). The two smallest species (*Eudyptula*; 1 kg) first reproduce at 2–3 years, do so once or twice a year, and have a two-egg clutch with nearly equal-sized eggs (Williams 1995). The 14 species of intermediate-sized penguins (*Pygoscelis*, *Spheniscus*, *Megadyptes*, and *Eudyptes*; 2–6 kg) first breed at 2–8 years, typically breed once a year, and have a two-egg clutch with either nearly equal-sized eggs (all non-*Eudyptes*) or extremely size-dimorphic eggs (*Eudyptes*). In *Pygoscelis*, *Spheniscus*, and *Megadyptes*, intraclutch ESD (mean = 2.1%, $n = 8$, calculated as $100 \times (|A - B|) \times [(A + B) \times 0.5]^{-1}$; table 1) is typical of other nonpasserine birds with altricial development (mean = 3.6%; Slagsvold et al. 1984). In *Eudyptes*, intraclutch ESD (mean = 36.8%, $n = 6$) is 17.5 times larger, on average, than that of other intermediate-sized penguins.

We assembled data for the 16 species of extant penguins with two-egg clutches (table 1; data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.cd233 [Stein and Williams 2013]). Specifically, we compiled species-specific mean values for adult female mass ($n = 16$), A-egg mass ($n = 12$), B-egg mass ($n = 12$), age of first reproduction ($n = 14$), chicks fledged per clutch ($n = 14$), and annual fecundity ($n = 14$). There is extensive interspecific variation in the duration of prelaying and
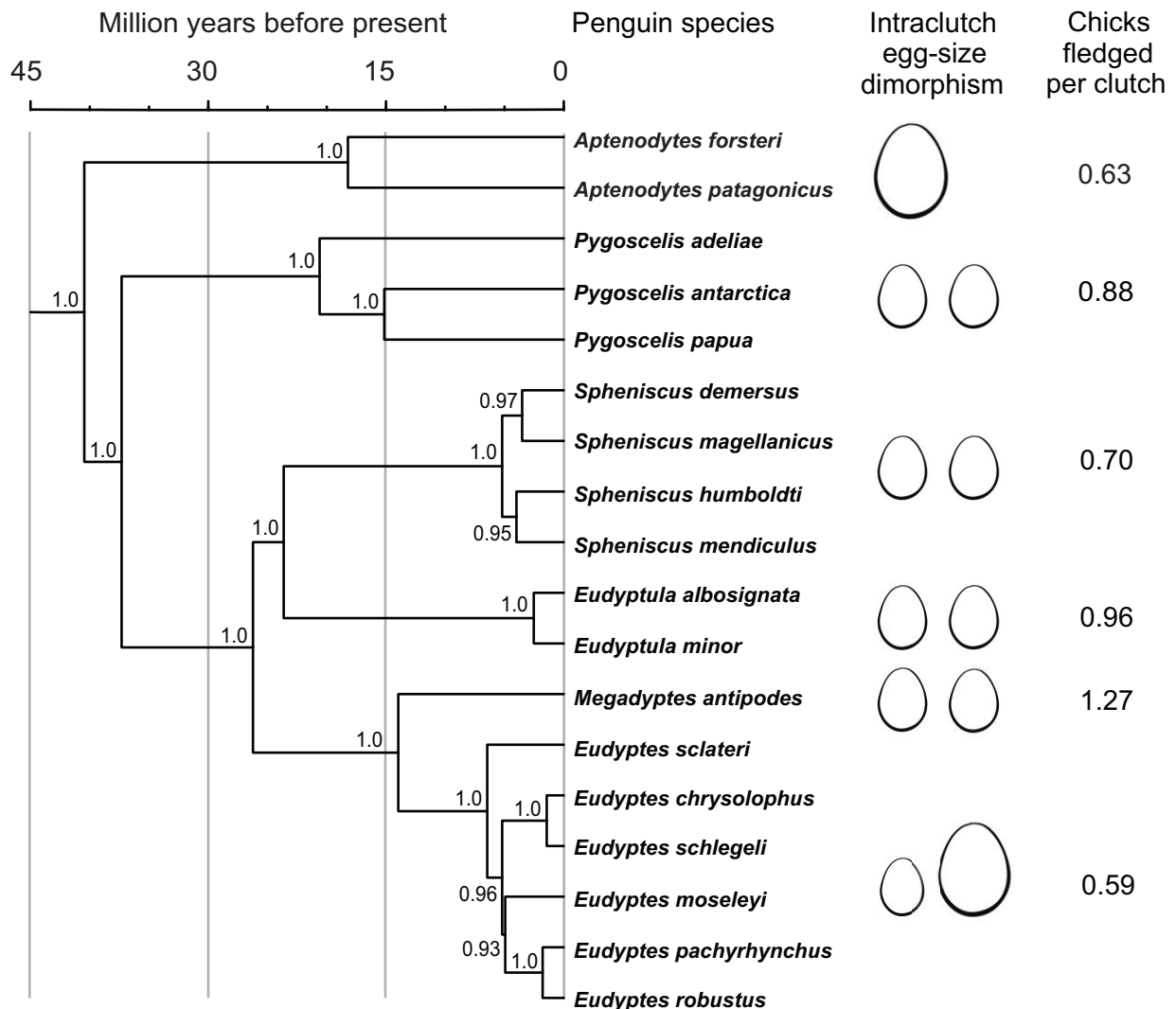
Figure 1: Time-calibrated molecular phylogeny of extant penguin species with Bayesian posterior support probabilities (from Baker et al. 2006). Extreme intraclutch egg-size dimorphism in *Eudyptes* is associated with evolutionary mismatch between clutch size and number of chicks fledged per clutch. *Aptenodytes patagonicus*, *Spheniscus mendiculus*, and *Eudyptes sclateri* are not included in genera means for chicks fledged per clutch.

incubation-related fasts, so adult female mass was taken from the chick-rearing period when birds are lean. There are no published data for fresh egg mass of *Spheniscus humboldti* (Peruvian penguin), *Spheniscus mendiculus* (Galapagos penguin), *Eudyptula albosignata* (white-flippered penguin), *Pygoscelis antarctica* (chinstrap penguin), and *Eudyptes robustus* (Snares penguin). Thus, we estimated fresh egg mass for these species (app. A). Age of first reproduction was averaged across males and females (females begin reproducing 0.5–1 years earlier than males) and was not adjusted for within-cohort mortality. *Eudyptula minor* (little penguin) and *S. humboldti* can success-

fully reproduce twice a year, so we distinguish between chicks fledged per clutch and chicks fledged annually. We do not consider adult or juvenile survival because most published survival estimates were generated with flipper tags, which can induce mortality in penguins (Saraux et al. 2011). We collected comparable data for *Aptenodytes forsteri* (emperor penguin), the only penguin species with a one-egg clutch and an annual reproductive cycle (Williams 1995); however, we restrict formal analyses to two-egg clutch species.

We used phylogenetic generalized least squares (PGLS; Pagel 1999; Freckleton et al. 2002) regression models to

Table 1: Life-history characteristics of penguin species used in comparative analyses and qualitative comparisons

Common name	Scientific name	Female mass (g)	A-egg mass (g)	B-egg mass (g)	Age of first reproduction (year)	Annual fecundity (chicks year⁻¹)	Chicks fledged per clutch (chicks clutch⁻¹)
Emperor	*Aptenodytes forsteri*	24,000[44]	469.4[44]	...	5.3[19]	.63[44]	.63[44]
Adélie	*Pygoscelis adeliae*	3,890[44]	122.8[44]	115.3[44]	5.8[1]	.99[1,21,32,34,36,46]	.99[1,21,32,34,36,46]
Gentoo	*Pygoscelis papua*	5,860[44]	128.2[44]	130.0[44]	3.5[19]	.83[6,27,30,41,43,44]	.83[6,27,30,41,43,44]
Chinstrap	*Pygoscelis antarctica*	3,893[44]	102.2[21]	102.5[21]	4.8[36]	.81[21,36]	.81[21,36]
Magellanic	*Spheniscus magellanicus*	3,708[2]	124.9[5]	124.7[5]	7.5[3]	.52[4,17,27,44,47]	.52[4,17,27,44,47]
Black-footed	*Spheniscus demersus*	2,880[24]	106.8[44]	104.8[44]	5.2[40]	.62[11]	.62[11]
Peruvian	*Spheniscus humboldti*	3,820[35]	121.2[10,44]	125.1[10,44]	2.5[48]	1.53[26]	.92[26]
Galapagos	*Spheniscus mendiculus*	1,768[44]	79.6[44]	80.9[44]	...	...	...
Little	*Eudyptula minor*	1,048[44]	53.7[20]	53.5[20]	2.6[13]	1.22[25,29]	.76[25,29]
White-flippered	*Eudyptula albosignata*	1,148[8]	60.0[8]	59.7[8]	2.6[8]	1.16[8]	1.16[8]
Yellow-eyed	*Megadyptes antipodes*	4,900[44]	139.4[22]	136.9[22]	3.2[31]	1.27[14,22,28]	1.27[14,22,28]
Erect-crested	*Eudyptes sclateri*	3,617[44]	81.6[15]	150.9[15]	...	...	...
Royal	*Eudyptes schlegeli*	4,100[39]	100.3[44]	159.3[44]	8.1[7]	.49[44]	.49[44]
Macaroni	*Eudyptes chrysolophus*	3,950[44]	92.7[44]	149.4[44]	7.5[12]	.49[33,42,45]	.49[33,42,45]
Rockhopper	*Eudyptes moseleyi*	2,290[9]	88.4[16]	118.4[16]	4.7[18]	.72[18]	.72[18]
Fiordland	*Eudyptes pachyrhynchus*	2,645[38]	99.4[44]	118.5[44]	5.5[35]	.50[38]	.50[38]
Snares	*Eudyptes robustus*	2,700[44]	103.3[23]	132.5[23]	6.3[37]	.77[44]	.77[44]

Source: (1) Ainley and Demaster 1980; (2) Bertellotti et al. 2002; (3) P. D. Boersma, personal communication, 2011; (4) Boersma et al. 1990; (5) Boersma et al. 2013; (6) Bost and Jouventin 1991; (7) Carrick and Ingham 1970; (8) C. N. Challies, personal communication, 2011; (9) Cherel et al. 1999; (10) R. Corado and L. S. Hall, unpublished data; (11) Crawford et al. 2006; (12) Croxall and Davis 1999; (13) Daan and Cullen 1990; (14) Darby and Seddon 1990; (15) Davis and Renner 2003; (16) Demongin et al. 2010; (17) Frere et al. 1998; (18) Guinard et al. 1998; (19) Jouventin and Weimerskirch 1981; (20) Kemp and Dann 2001; (21) Lishman 1985; (22) M. Massaro, personal communication, 2010; (23) Massaro and Davis 2005; (24) Nagy et al. 1984; (25) Nisbet and Dann 2009; (26) Paredes et al. 2002; (27) Putz et al. 2001; (28) Ratz et al. 2004; (29) Reilly and Balmford 1975; (30) Reilly and Kerle 1981; (31) Richdale 1957; (32) Spurr 1975; (33) Stahl 1985; (34) Taylor 1962; (35) Taylor et al. 2002; (36) Trivelpiece et al. 1990; (37) Warham 1974*a*; (38) Warham 1974*b*; (39) Warham 1971; (40) Whittington 2005; (41) Williams 1980*a*; (42) Williams 1980*b*; (43) Williams 1991; (44) Williams 1995; (45) Williams and Croxall 1991; (46) Yeates 1968; (47) Yorio 2001; (48) C. B. Zavalaga and R. Paredes, personal communication, 2009.

Note: Female mass: all single-study data points taken from the chick-rearing period, except for the following: (1) *E. schlegeli*, midpoint of range 3,200–5,000 g; (2) *E. minor*; (3) *Pygoscelis antarctica*, mean of three studies. A- and B-egg mass: all single-study data points, except for the following: (1) *E. pachyrhynchus*, mean of two studies; (2) *E. chrysolophus*, mean of 3 years, South Georgia Island; (3) *P. adeliae*, mean of two studies; (4) *S. humboldti*, unpublished data; (5) A- and B-egg mass for *P. antarctica*, *S. humboldti*, *S. mendiculus*, *E. albosignata*, and *E. robustus* was estimated using an ordinary least squares regression equation derived from fresh egg mass of 10 two-egg clutch penguins species (fresh egg mass = $-1.28 + 1.08 \times$ length $\times$ breadth$^2 \times \pi \times 6^{-1}$, $F_{1,18} = 7,080$, $P < .0001$, adjusted $r^2 = 0.997$; for details, see app. A). Age of first reproduction: average of male and female mean ages of first reproduction uncorrected for within-cohort mortality. Annual fecundity: values for *S. humboldti* and *E. minor* account for successful second clutches.

test for a life-history slowdown, evolutionary mismatch, and their interaction. PGLS is analogous to ordinary least squares regression in that the error distribution is Gaussian; however, in PGLS the independence assumption is relaxed (Freckleton et al. 2002). The lack of independence among taxa is accounted for in PGLS by incorporating phylogenetic covariance directly; this sets the expected residual correlation structure (Freckleton et al. 2002). We use a well-supported, dated molecular phylogeny to specify phylogenetic covariance among penguins (fig. 1; Baker et al. 2006). We modeled character evolution with Pagel's (1999) correlation structure, which assumes constant variance through time. Pagel's (1999) methodology provides a maximum likelihood estimate of phylogenetic autocorrelation, λ, which specifies the optimal branch length transformation for correlated characters (Freckleton et al. 2002). Character evolution is independent of phylogeny when $\lambda = 0$ and conforms exactly to Brownian motion when $\lambda = 1$. When $0 < \lambda < 1$, the influence of phylogeny

is weaker than strict Brownian motion (Freckleton et al. 2002). When closely related species have inversely related characters, $\lambda < 0$.

We use adult female mass as a size covariate and transform variables logarithmically (base *e*) where appropriate. We characterize ESD as the mass difference between B- and A-eggs. We use dummy variables, coded as 0 or 1, to distinguish *Eudyptes* and non-*Eudyptes* penguins and to assess variation in ESD within *Eudyptes*. Tests of predictions are reported with one-tailed *P* values, and test statistics associated with covariates are reported with two-tailed *P* values; α is set at 0.05, and parameter estimates are reported with standard errors. All analyses were conducted in APE (Paradis et al. 2004; R Development Core Team 2011).

Results

Consistent with life-history theory, annual fecundity was inversely correlated with age of first reproduction (fig. 2;
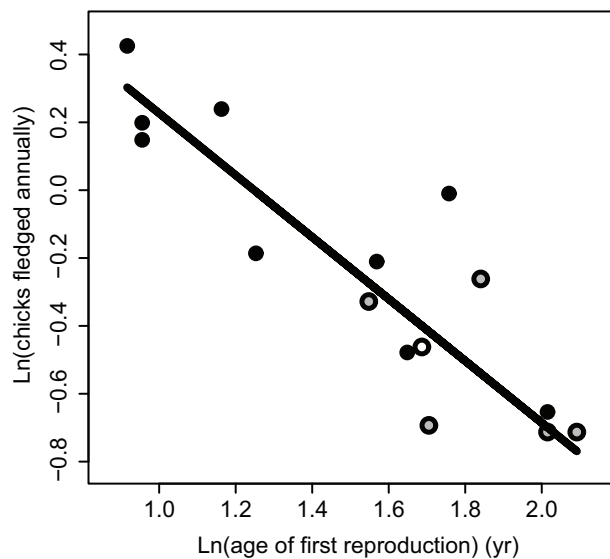
Figure 2: Phylogenetic generalized least squares regression model demonstrating a uniform, inverse relationship between annual fecundity and age of first reproduction for two-egg clutch penguin species. Gray circles represent *Eudyptes*, and black circles represent *Pygoscelis, Spheniscus, Eudyptula,* and *Megadyptes*. White circle represents *Aptenodytes fosteri*, the only extant one-egg clutch penguin species with a annual reproductive cycle. *Aptenodytes fosteri* was not included in the analysis and is displayed only for comparison.

$\lambda = -0.20$, $\beta_{\ln(\text{age of first breeding})} = -0.91 \pm 0.13$, $n = 14$, $t_{11} = -6.8$, $P < .0001$), even while accounting simultaneously for adult female body mass ($t_{11} = 1.14$, $P > .2$). This inverse relationship was homogeneous across *Eudyptes* and non-*Eudyptes* taxa (interaction: $\lambda = -0.22$, $n = 14$, $t_9 = 0.26$, $P > .8$; dummy variable: $\lambda = -0.22$, $t_{10} = -1.29$, $P > .2$). Consistent with a life-history slowdown in *Eudyptes*, age of first reproduction was 52% later ($\lambda = 0.02$, $n = 14$; *Eudyptes* vs. non-*Eudyptes*: 6.4 ± 0.8 vs. 4.2 ± 0.6 years, $t_{12} = 2.41$, one-tailed $P = .016$) and annual fecundity 48% lower ($\lambda = -0.47$, $n = 14$, 0.50 ± 0.09 vs. 0.96 ± 0.02 chicks fledged year^{-1}, $t_{12} = 4.57$, one-tailed $P = .0003$) than those of other two-egg clutch penguin species. Consistent with an evolutionary mismatch between clutch size and realized fecundity, *Eudyptes* also fledged 43% fewer chicks per two-egg clutch ($\lambda = 0.52$, $n = 14$, 0.52 ± 0.17 vs. 0.91 ± 0.11 chicks fledged two-egg clutch^{-1}, $t_{12} = 2.27$, one-tailed $P = .0211$).

It is unclear whether extreme intraclutch ESD in *Eudyptes* resulted from a decrease in relative A-egg size, an increase in relative B-egg size, or a combination of the two. Here we characterize A- and B-egg allometry for the two-egg clutch Spheniscidae. A-egg allometry differs markedly between *Eudyptes* and non-*Eudyptes* taxa (fig.

3A; $\lambda = 0.93$, $n = 16$; interaction: $t_{12} = 3.92$, $P < .0020$; dummy variable: $t_{12} = 3.77$, $P < .0027$). A-egg allometry is positive in non-*Eudyptes* taxa ($\beta_{\ln(\text{female mass})} = 0.57 \pm 0.06$, $t_{12} = 8.81$, $P < .0001$) but not in *Eudyptes* ($\beta_{\ln(\text{female mass})} = 0.01 \pm 0.13$, $t_{12} = 0.09$, $P > .9$). B-egg allometry is positive and uniform across two-egg clutch Spheniscidae (fig. 3B; $\lambda = 0.83$, $n = 16$; interaction: $t_{12} = -0.65$, $P > .5$, $\beta_{\ln(\text{female mass})} = 0.57 \pm 0.04$, $t_{12} = 13.83$, $P < .0001$); however, relative B-egg size is uniformly larger in *Eudyptes* ($\lambda = 0.83$, $n = 16$; $\beta_{\ln(\text{dummy variable})} = 0.27 \pm 0.05$, $t_{13} = 4.92$, $P < .0004$). The striking difference between A- and B-egg allometry suggests that variation in ESD within *Eudyptes* may be attributable, in part, to the A-egg interaction. To characterize the contribution of the A-egg to variation in ESD, we divided the six *Eudyptes* species into two groups on the basis of deviation from A-egg allometry of non-*Eudyptes* taxa (fig. 3A): the three larger species (*Eudyptes sclateri, Eudyptes chrysolophus,* and *Eudyptes schlegeli*) have large negative deviations, while the three smaller species (*Eudyptes moseleyi, Eudyptes pachyrhynchus,* and *Eudyptes robustus*) have small positive deviations (fig. 3A). Compared with non-*Eudyptes* taxa, relative A-egg size is smaller in the three larger ($\lambda = 0.96$, $n = 16$; dummy variable: $t_{12} = -3.79$, $P < .0026$) but not in the three smaller (dummy variable: $t_{12} = 0.24$, $P > .8$) *Eudyptes* species. Variation in ESD within *Eudyptes* is attributable to a 5.4% increase in relative B-egg size across the genus (fig. 3B) and to a 5.6% decrease in relative A-egg size in the three larger species (fig. 3A).

Finally, we test whether the evolution of intraclutch ESD in two-egg clutch Spheniscidae can be explained by an interaction between a life-history slowdown and evolutionary mismatch. Intraclutch ESD was independent of female mass ($\lambda = 2.29$, $n = 14$, $t_{12} = -0.45$, $P > .7$) and mean egg mass ($\lambda = 2.24$, $n = 14$, $t_{12} = -0.39$, $P > .7$), so these potential size covariates were excluded from models explaining ESD. As expected, intraclutch ESD was positively correlated with age of first reproduction in *Eudyptes* but not in other two-egg clutch penguin species (fig. 4; $\lambda = -0.47$, $n = 14$; interaction: $\beta_{(\text{age of first reproduction: dummy variable})} = 9.62 \pm 2.46$, $t_{10} = 3.91$, one-tailed $P = .0015$; main effects: $\beta_{(\text{age of first reproduction})} = -0.44 \pm 1.08$, $t_{10} = -0.41$, $P > .6$; $\beta_{(\text{dummy variable})} = -23.08 \pm 13.85$, $t_{10} = -1.67$, $P > .1$).

Discussion

Lack (1968) suggested that extreme intraclutch ESD in *Eudyptes* penguins might represent a rare, transitional stage in the evolution of a one-egg clutch, and we provide life-history context for this prescient observation. Consistent with the evolution of a slower life history in *Eudyptes*, age of first reproduction is 52% later and annual fecundity 48% lower compared with non-*Eudyptes* taxa. Despite this
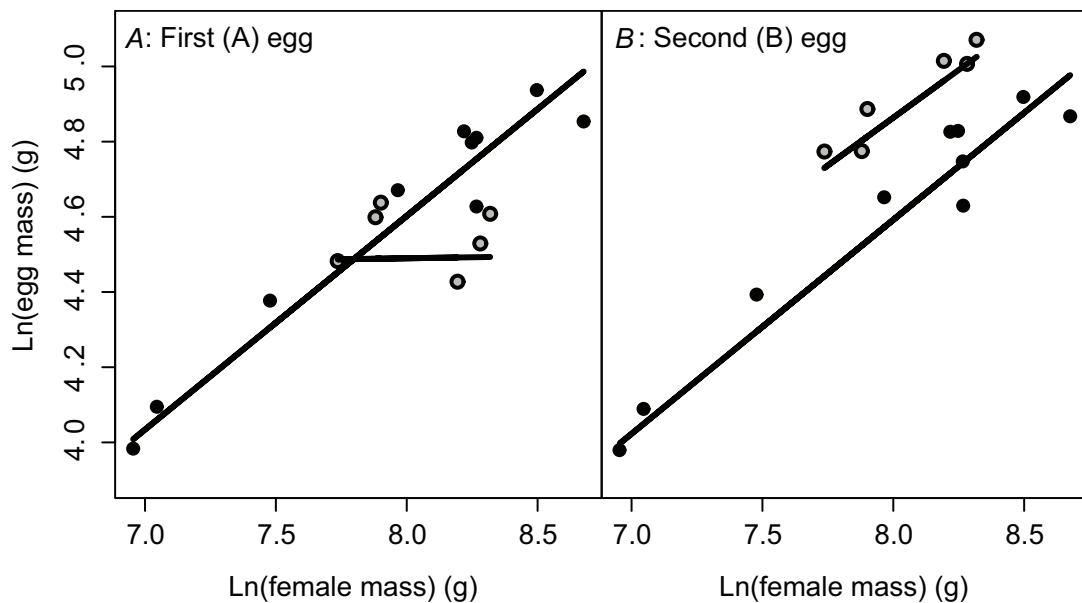
Figure 3: Phylogenetic generalized least squares regression models depicting A-egg (*A*) and B-egg (*B*) allometry for two-egg clutch penguin species. Gray circles represent *Eudyptes*, and black circles represent *Pygoscelis*, *Spheniscus*, *Eudyptula*, and *Megadyptes*. For consistency, the full regression model (interaction and main effects) is plotted in each panel.

marked life-history slowdown, clutch size has not decreased in *Eudyptes* as expected: all six species retain a two-egg clutch. The apparent inconsistency between a slowdown in some life-history traits (age of reproduction and annual fecundity) but not in others (clutch size) is reinforced by comparison with the emperor penguin *Aptenodytes forsteri*, the only penguin species with a one-egg clutch and an annual reproductive cycle (Williams 1995). Although *A. forsteri* is 7.5-times larger on average than *Eudyptes* taxa (table 1), relative egg size (calculated as $(\log_e(\text{egg mass}) \times \log_e(\text{female mass})^{-1}$; *Eudyptes* mean $\pm$ SE vs. *A. forsteri*; B-egg: 0.611 ± 0.002 vs. 0.610) and annual fecundity (0.59 ± 0.06 vs. 0.63 chicks year^{-1}) are remarkably similar. However, age of first reproduction is actually 18.5% later on average in *Eudyptes* (6.4 ± 0.6 vs. 5.4 years). It is not possible to infer whether the *Aptenodytes* lineage evolved from a one- or two-egg clutch ancestor because the sister group to Spheniscidae, Ciconiidae (storks), is too distantly related to be informative (diverged ~67 million years before present; Pacheco et al. 2011). However, the current breeding distribution and unique life-history characteristics of *Aptenodytes* (winter breeding, foot incubation, extremely prolonged chick rearing; Williams 1995) suggest that *Aptenodytes* evolved under a different selective regime than *Eudyptes*.

The similarities in life history between *A. forsteri* and *Eudyptes* taxa raise an important question: why have all six species in *Eudyptes* failed to evolve a one-egg clutch?

The extant radiation of *Eudyptes* penguins diversified ~7 million years before present (Baker et al. 2006) and contains >26 million years of evolutionary history (sum of branch lengths within *Eudyptes*; fig. 1). Retention of a two-egg clutch across a marked life history slowdown, five speciation events, and >26 million years of evolutionary history suggests that a two-egg clutch became canalized before the diversification of the extant *Eudyptes* taxa (see below). This raises a related question: how should egg size evolve when clutch size is canalized and life history slows down? Comparison with *A. forsteri* indicates that B-egg size is exactly what one would predict if *Eudyptes* penguins had a one-egg clutch; this corroborates Williams (1990) suggestion that B-egg size might be optimized to enhance survival in a one-chick brood. A-egg size has decreased in the three *Eudyptes* species with the most extreme ESD, and this may provide a means of reducing costs of A-egg production in these species. Variation in intraclutch ESD is positively correlated with age of first reproduction in *Eudyptes* but not in other two-egg clutch penguin species; this suggests that extreme intraclutch ESD arose in *Eudyptes* as a consequence of an interaction between selection favoring a slower life history and clutch size canalization.

Penguins have the slow life histories characteristic of pelagic seabirds (Weimerskirch 2002), and intraspecific clutch-size invariance is ubiquitous among pelagic seabirds (Hamer et al. 2002; *Procellariiformes* [125 species; one egg], *Sphenisciformes* [18 species; one or two eggs), *Charadri-*
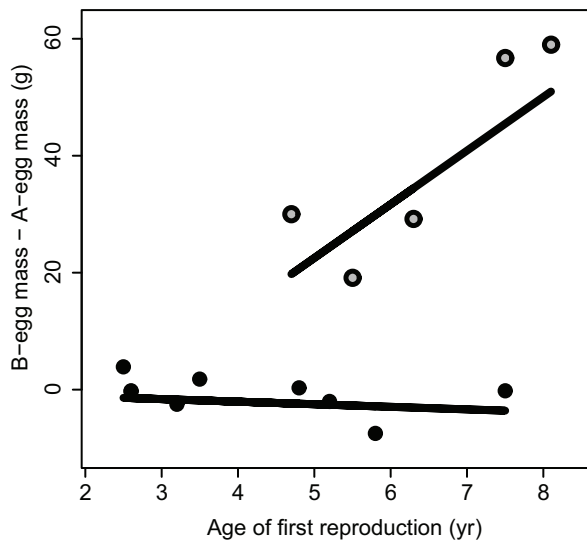
Figure 4: Phylogenetic generalized least squares regression model explaining egg-size dimorphism (B-egg mass − A-egg mass) for two-egg clutch penguin species. Egg-size dimorphism is positively correlated with age of first reproduction in *Eudyptes* but not in other two-egg clutch penguin species. Gray circles represent *Eudyptes*, and black circles represent *Pygoscelis*, *Spheniscus*, *Eudyptula*, and *Megadyptes*.

iformes (Alcidae: 22 species; one or two eggs; Laridae: 55 species; one, two, or three eggs). So why is extreme intraclutch ESD restricted to Spheniscidae and specifically to *Eudyptes*? We suggest that the answer to this question involves a combination of particularly high migration-related costs in penguins and limited opportunities for the evolution of extreme intraclutch ESD in pelagic seabirds. Extreme intraclutch ESD requires clutch size >1. Clutches of two and three eggs are relatively rare in pelagic seabirds (Hamer et al. 2002), and this suggests that there have been limited opportunities for extreme intraclutch ESD to evolve. Penguins are flightless, and flipper-propelled swimming is an expensive means of transport. Field metabolic rate of penguins is intermediate among seabirds (doubly labeled water estimates; Shaffer 2011); however, mean swimming speed (2.1 m s^{-1}, $n = 7$; Croxall and Davis 1990) of penguins is 82% slower than mean ground speed (11.8 m s^{-1}, $n = 25$; Spear and Ainley 1997) of other pelagic seabirds. Intermediate energy expenditure coupled with slow travel speed suggest that the energetic and temporal costs of migration are exceptionally high in the Spheniscidae, and this has been confirmed empirically for *Eudyptes* (Bost et al. 2009; Green et al. 2009). We would expect high temporal and energetic costs of migration in *Eudyptes* to exert strong, persistent stabilizing selection on the timing of life-history events.

Eudyptes penguins are characterized by high primary

reproductive investment (two-egg clutch) but low realized fecundity (0.59 ± 0.06 chicks year^{-1}). This aberrant trait combination provides a rare example of evolutionary mismatch and offers novel support to the interpretation that *Eudyptes*' two-egg clutch is maladaptive (sensu Crespi 2000). Failure to evolve a one-egg clutch in *Eudyptes* would be less problematic if production costs of the extra egg were negligible, and it has been argued that this is the case, given that A-egg mass represents only 2%–5% of adult female mass (table 1; Williams 1995). However, the assessment of low production costs considers only the direct energetic costs of the A-egg. In *Eudyptes*, egg formation is associated with prolonged fasting (35–40 days) and extreme mass loss (30% of arrival mass in female *Eudyptes chrysolophus*; Williams 1995). A pair of *E. chrysolophus* loses a minimum of 11.5 incubation-day equivalents (14,000 kJ) of body reserves to A-egg production, and this represents 33% of the 35-day incubation period (app. B). While we acknowledge that constraint-based arguments are open to criticism, it is interesting, albeit anecdotal, that when *E. chrysolophus* is maintained in captivity (abundant food resources, low energetic demands, and no migration) and allowed to incubate eggs and raise chicks systematic, early loss of the A-egg persists ($n = 7$), and fledging success remains low (0.43 ± 0.20 chicks per two-egg clutch; $n = 7$; R. W. Stein, unpublished data). If a two-egg clutch coupled with extreme intraclutch ESD is part of an adaptive strategy evolved to exploit rare times of abundant resources, then we would expect a highly flexible response to exploit those opportunities, but this has not been observed in captives. Taken together, these novel lines of evidence provide support for the interpretation that the persistence of a two-egg clutch might not be part of an adaptive strategy.

We suggest that *Eudyptes*' extreme intraclutch ESD evolved in the context of clutch-size invariance (a canalized two-egg clutch) stemming from a unique interaction between the physiology of follicle (yolk) development and selection favoring a slower life history that resulted in temporal overlap between migration and reproduction (Crossin et al. 2010). In birds, including penguins, the number of recruited follicles exceeds clutch size, and pre-ovulatory follicles are resorbed after clutch completion (Haywood 1993; Crossin et al. 2011). Clutch size is typically determined by arresting follicle development at the end of the follicle hierarchy (Haywood 1993), not by selective abortion of earlier developing follicles within the hierarchy (Goerlich et al. 2010). In penguins, development of the A-follicle precedes that of the B-follicle by ~4 days (Grau 1982; Astheimer and Grau 1985; Crossin et al. 2010); this suggests that development of the A-follicle will be disproportionately affected by migration overlap, with migration overlap potentially contributing to the extent of

ESD (Crossin et al. 2010). Consistent with this, *Eudyptes pachyrhynchus* exhibits the lowest ESD (17.5%) within *Eudyptes* and little or no overlap between follicle development and migration (Grau 1982; Williams 1995), while *E. chrysolophus* exhibits among the highest ESD (46.8%) and extensive overlap between follicle development and migration (Williams 1990; Crossin et al. 2010). There is a widespread fitness advantage associated with early onset of egg laying in birds (Williams 2012). If this fitness advantage was large when *Eudyptes* made the transition to a pelagic overwintering ecology and their life history slowed down, then selection could have favored migration-reproduction overlap, with the energetic cost of the A-egg being offset by the increased survival probability of the B-chick. Under such a selective regime, the physiology of clutch-size determination could favor the B-egg and preclude the subsequent elimination of the A-follicle.

In conclusion, the six species of *Eudyptes* penguins have an invariant two-egg clutch but attempt to raise only one chick (Williams 1995); this bizarre combination of reproductive traits constitutes a genus-wide evolutionary mismatch between clutch size and realized fecundity. This mismatch is associated with reversed hatching asynchrony (St. Clair 1996) and maternal egg ejection (St. Clair et al. 1995), which appear to have coevolved with extreme intraclutch ESD in *Eudyptes*. Reversed hatching asynchrony ensures systematic loss of the A-chick when the smaller A-egg is retained until hatching (St. Clair 1992, 1996). Maternal egg ejection typically occurs at or before the time the B-egg is laid (St. Clair et al. 1995). While acknowledging that our constraint-based explanation is controversial, we argue that an invariant two-egg clutch coupled with extreme intraclutch ESD, high production costs of the A-egg, systematic loss of the A-egg or A-chick (in the wild), and an apparent inability of abundant food resources to rescue the A-egg or A-chick (in captivity) are more consistent with maladaptation than they are with an adaptive strategy. We suggest that the persistent failure to evolve a one-egg clutch constitutes a genus-wide evolutionary maladaptation unique to *Eudyptes* and that extreme intraclutch ESD arose as a correlated response to selection favoring a slower life history.

APPENDIX A

Estimation of Fresh Egg Mass from Linear Dimensions

Because of a lack of published fresh egg mass data, we estimated A- and B-egg mass for *Spheniscus humboldti* (Peruvian penguin), *Spheniscus mendiculus* (Galapagos penguin), *Eudyptula albosignata* (white-flippered penguin), and *Eudyptes robustus* (Snares penguin). To do this, we assembled species-specific ($n = 10$) mean length, breadth, and mass measurements taken from the same set of fresh eggs ($n \geq 20$ for each species; table A1). Penguin eggs are roughly ellipsoid, so we calculated egg volume = length × breadth^2 × π × 6^{-1} and assumed that A-egg and B-egg volumes provide independent estimates of egg mass. Visual inspection revealed a pair of points, A- and B-eggs of *Pygoscelis antarctica*, that deviated strongly from an otherwise exceptionally tight linear relationship (data not shown); both eggs were ~10 g larger than expected from their linear dimensions (A-egg residual = 4.1, Bonferroni $P = .0140$; B-egg residual = 6.4, Bonferroni $P = .0001$). After first confirming that the dimensions reported by Lishman (1985) were likely correct (Belliure et al. 1999), we excluded *P. antarctica* from the regression analysis and estimated A- and B-egg mass for this species also.

The resulting ordinary least squares regression equation was adequate for prediction (fresh egg mass = $-1.28 \pm 1.32 + 1.08 \pm 0.01 \times$ calculated volume, $n = 20$, $F_{1,18} = 7,080$, $P < .0001$, adjusted $r^2 = 0.997$). Egg dimensions for the five species requiring egg mass estimation were within the range of the 10 species included in the regression. We validated our egg mass estimation to assess bias. First, we retained the species with the largest (*Eudyptes schlegeli*) and smallest (*Eudyptula minor*) eggs and iteratively excluded each of the eight remaining species. Second, we used the ordinary least squares regression equation from each set of nine species to estimate A- and B-egg mass for the one excluded species. Finally, we compared estimated and fresh egg mass for the one excluded species. The mean difference between estimated and fresh mass was +0.26% for A-eggs and −0.30% for B-eggs. Thus, we are confident that egg

Table A1: Species and sample sizes of A- and B-eggs used to estimate fresh egg mass from linear dimensions

Common name	Scientific name	A-egg (n)	B-egg (n)	Source
Adélie	*Pygoscelis adeliae*	73	73	Lishman 1985
Gentoo	*Pygoscelis papua*	20	20	Williams 1995
Chinstrap	*Pygoscelis antarctica*	51	56	Lishman 1985
Black-footed	*Spheniscus demersus*	70	70	Williams 1995
Little	*Eudyptula minor*	94	94	Kemp and Dann 2001
Erect-crested	*Eudyptes sclateri*	50	50	Williams 1995
Royal	*Eudyptes schlegeli*	31	28	Williams 1995
Macaroni	*Eudyptes chrysolophus*	52	70	Williams 1995
Northern rockhopper	*Eudyptes moseleyi*	122	119	Williams 1995
Eastern rockhopper	*Eudyptes filholi*	37	37	Williams 1995
Fiordland	*Eudyptes pachyrhynchus*	54	54	Williams 1995

Note: Published fresh mass for the A- and B-eggs of *P. antarctica* was almost exactly 10 g larger than expected from linear dimensions. Thus, *P. antarctica* was excluded from the predictive analysis, and fresh egg mass was also estimated for this species.

mass estimation did not strongly influence the results presented here.

APPENDIX B

Costs of A-Egg Production: Time and Energy

Inferring that *Eudyptes*' two-egg clutch constitutes a genus-wide evolutionary maladaptation is contingent on high production costs for the A-egg. Here, we quantify the direct and indirect energetic costs of A-egg production for *Eudyptes chrysolophus* and, using the incubation metabolic rate (1,242.9 kJ day^{-1}; Brown 1984), represent these costs as incubation-day equivalents. The A-egg of *E. chrysolophus* is composed of 14.1 g yolk and 5.7 g albumen (dry matter; Crossin et al. 2010). Assuming that the yolk is composed of 58% lipid and 42% protein (*Eudyptes pachyrhynchus*; Grau 1982), that lipid and protein contain 38.91 and 17.99 kJ g^{-1}, respectively (Whittow 1986), and 75% conversion efficiency, the direct cost of A-egg production is 703 kJ and constitutes 0.6 incubation-day equivalents. Indirect costs accrue across males and females because all *Eudyptes* taxa have shared incubation (Williams 1995). During the 4.2-day laying interval, female *E. chrysolophus* metabolize 342.5 g of reserves, which are composed of 35.3% water, 55.5% lipid, and 9.2% protein (Croxall 1982). The 7,998.5 kJ of metabolized reserves constitute 6.4 incubation-day equivalents. Comparable mass loss data are not available for males; however, assuming an average daily metabolic rate of 1,319.6 kJ × d^{-1} (Brown 1984), which is ~6% higher than the incubation metabolic rate, males lose 4.5 incubation-day equivalents during the laying interval (potentially decreasing the probability of successfully retuning to relieve their partner). In an *E. chrysolophus* pair, 11.5 incubation-day equiv-

alents are lost to A-egg production, and this represents 33% of the 35-day incubation period. This estimate represents the minimum production costs because energetic, temporal, and survival costs associated with foraging to attain the lost reserves are not included, nor is the temporal cost of the laying interval.

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