

ONTOGENY OF LARGE BIRDS: MIGRANTS DO IT FASTER

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Abstract. We compared incubation and fledging times between large (>2 kg) migrating and sedentary birds. We found that while length of incubation period does not differ between migrants and nonmigrants, fledging period is significantly shorter in the former. This pattern is apparent in the class as a whole, as well as within orders, families, and genera. Additional, albeit weak, evidence suggests that clutch sizes of migrants are smaller than those of closely related resident birds. We hypothesize that the need to migrate constrains the length of developmental period of large migrating birds, especially in species that undertake long-distance migration.

Key words: *body size, constraints, development, fledging, incubation, migration.*

Ontogenia de Aves Grandes: Los Migrantes lo Hacen más Rápido

Resumen. Comparamos los tiempos de incubación y emplumamiento entre aves grandes (>2 kg) migratorias y sedentarias. Encontramos que mientras la longitud del período de incubación no difiere entre migrantes y no migrantes, el período de emplumamiento es significativamente más corto en las migrantes. Este patrón resulta evidente a nivel de toda la clase, así como al interior de órdenes, familias y géneros. Existe evidencia adicional, aunque débil, que sugiere que las nidadas de las migrantes son más pequeñas que las de aves residentes estrechamente relacionadas. Proponemos la hipótesis de que la necesidad de migrar limita la longitud del período de desarrollo de las aves migrantes grandes, especialmente en las especies que realizan migraciones a través de grandes distancias.

INTRODUCTION

A bird's breeding cycle consists of the periods of courtship, nest building, egg laying, incubation, and fledging. Many biological characters, including the length of incubation and fledging periods, scale positively with body mass (Rahn et al. 1975, Calder 1984, Schmidt-Nielsen 1984). It is therefore obvious that the larger a bird is, the longer it needs to develop from a zygote to a flying juvenile. Juveniles of some large birds do indeed require a long period before taking first flight: the combined incubation and fledging periods for the Andean Condor (*Vultur gryphus*) and the Californian Condor (*Gymnogyps californianus*) are 239 and 238 days, respectively; and developmental periods in excess of 300 days have been recorded for the larger species of albatrosses (del Hoyo et al. 1992). The flightless King Penguin (*Aptenodytes patagonicus*; 13.2 kg, Dunning 1993), which breeds close to its feeding grounds, has a development period of just over a year (385 days; del Hoyo et al. 1992, Reilly 1994), perhaps the

longest of any bird. Its far larger congener, the 34-kg Emperor Penguin (*A. forsteri*; Dunning 1993), feeds in Antarctic waters but breeds inland. This species starts its breeding cycle in the Antarctic winter, and its chicks attain adult plumage 214 days after incubation begins (del Hoyo et al. 1992, Reilly 1994). Could it be that the migratory behavior of the Emperor Penguin forces it to shorten its development time, relative to its smaller, sedentary congener?

Whereas chicks of migratory birds need to complete their growth and gain flight capability by fall, long developmental periods pose little problem for sedentary birds. Large migratory birds with a long breeding cycle would thus be at a disadvantage in high latitudes, where the breeding season is short. Members of large migratory species might therefore have accelerated their development in comparison with similar-sized residents. A short breeding season at high latitude, combined with high wing load and a consequent reduction in speed of flapping flight might explain why large birds do not migrate very long distances (Hedenström and Ålerstam 1998).

Several factors affect the length of avian developmental periods. For example, woodpeckers

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(Picidae) and other cavity nesters usually have shorter incubation and longer fledging times compared to similar-sized noncavity nesters (Yom-Tov and Ar 1993). Similarly, shearwaters (Procellariidae) have a very long fledging period, whereas game birds (Galliformes) fledge early in relation to other birds (Carrier and Auriemma 1992).

Long-distance migrants have small clutches and raise fewer broods per year than do residents, while short-distance migrants have the most broods per year and the smallest clutches among these three groups (Böhning-Gaese et al. 2000). Large birds usually lay only one clutch per year, and are therefore unable to shorten their breeding cycle by having fewer clutches. They can, however, shorten it by shortening the periods of courtship behavior, nest building, egg laying, incubation and fledging. Since the latter two periods are generally the longest in the breeding cycle, it is reasonable to assume that plasticity in length of the breeding cycle would be reflected mostly through changes in these parameters. Therefore we designed this study to examine whether large migratory birds respond to the selective pressure to complete their growth quickly by accelerating their nesting cycle relative to similar-sized nonmigratory species.

METHODS

We obtained the data for mean clutch size, length of incubation and fledging periods, and migratory habits of large (over 2 kg) flying birds from del Hoyo et al. (1992). Data for the Greater Spotted Eagle are from Graszynski et al. (2002; scientific names appear in Table 1). Members of the Galliformes and Otididae, whose chicks are capable of flying well before they attain adult size (Carrier and Auriemma 1992, Collar 1996), were not considered. Species in which some populations migrate whereas others do not (such as Golden Eagle and Canada Goose) were not used, as the developmental periods listed for these species do not note whether they refer to migratory or nonmigratory populations.

The choice of 2 kg for classifying a bird as large was somewhat arbitrary, considering that the modal size in the class Aves is much lower (33 g, Maurer 1998). However, we expected that birds with body mass smaller than 2 kg would have developmental periods far shorter than the length of the respective breeding season. Using

a larger threshold for "large" birds would have prevented us from controlling for phylogeny in comparing migrant and sedentary species. It should be noted, however, that we do not mean to imply that 2 kg is the precise threshold for differences in developmental periods between migrant and sedentary species.

Body-mass data (of the larger sex where available) were obtained from Dunning (1993) and del Hoyo et al. (1992). We followed the taxonomy of del Hoyo et al. (1992). We calculated development time as the sum of incubation and fledging periods (in days). Some large birds have a long postfledging period, leading to an underestimate of actual developmental periods. Our data show that such postfledging periods (which can be up to a year long, especially in large raptors such as the Martial Eagle or the Great Philippine Eagle, del Hoyo et al. 1992) are almost invariably restricted to sedentary species. Because precise data on postfledging care are often lacking we have taken a conservative approach, and added such data to the calculated developmental times only for species of *Pelecanus*, the only genus in our data in which postfledging care exists in migrants.

Another factor influencing the length of the nesting period is that of time taken to lay the entire clutch. In order to examine whether laying time differs between migrant and sedentary species (as was found for clutch size, Böhning-Gaese et al. 2000), clutch size must be multiplied by the interval between the laying of successive eggs. However, to the best of our knowledge data on the latter variable are nearly nonexistent for the species in our sample. We therefore used clutch size only as a surrogate for the length of the laying period. Because clutch size is highly dependent on phylogenetic relationships, we analyzed this effect by using only families containing both migrant and sedentary species. We used a two-way ANOVA, with clutch size as the dependent variable, and both family and migration as the categorical predictors.

Species may not constitute independent data points, owing to shared phylogeny (Smith 1994); thus comparing all large birds regardless of phylogeny runs the risk of inflating the number of actual degrees of freedom. This is not merely a statistical problem: different bird taxa occupy different positions along the altricial-precocial continuum, which greatly influences developmental rates and times (Ricklefs and

TABLE 1. Body mass, clutch size, length of incubation and fledging periods, and migratory habits of all large (>2 kg) birds with known development times (del Hoyo et al. 1992). Species with precocial flight and species with both migratory and sedentary populations are excluded. Taxonomy and common names follow del Hoyo et al. (1992). Superscripts denote migrant-resident pairs of closely related species, used for pairwise comparisons to account for phylogeny.

Common name	Scientific name	Mass (g)	Clutch size	Incubation period (days)	Fledging period (days)	Migratory?
Anatidae						
Egyptian Goose	<i>Alopochen aegyptiacus</i>	2100	8.5	29	68	no
Greater White-fronted Goose	<i>Anser albifrons</i> ¹	2700	5.5	25	42	yes
Pink-footed Goose	<i>Anser brachyrhynchus</i>	2750	4	27	56	yes
Snow Goose	<i>Anser caerulescens</i>	3450	4.5	24	45	yes
Emperor Goose	<i>Anser canagicus</i>	2750	5	25	55	yes
Bean Goose	<i>Anser fabalis</i>	3200	5	28	40	yes
Bar-headed Goose	<i>Anser indicus</i>	2600	5	29	53	yes
Magpie Goose	<i>Anseranas semipalmata</i>	2050	8.5	24	77	no
Hawaiian Goose	<i>Branta sandvicensis</i> ¹	2000	4	29	77	no
Cape Barren Goose	<i>Cereopsis novaehollandiae</i>	3550	5	36	73	no
Andean Goose	<i>Chloephaga melanoptera</i>	2900	7.5	30	84	no
Black Swan	<i>Cygnus atratus</i> ²	6200	6.5	38	160	no
Trumpeter Swan	<i>Cygnus buccinator</i>	11 400	6	35	102	yes
Tundra Swan	<i>Cygnus columbianus</i> ²	7100	4	31	68	yes
Whooper Swan	<i>Cygnus Cygnus</i>	9350	4.5	35	87	yes
Mute Swan	<i>Cygnus olor</i>	11 800	6	36	135	yes
Spur-winged Goose	<i>Plectropterus gambensis</i>	3550	10	32	70	no
Comb Duck	<i>Sarkidiornis melanotos</i>	2600	13	29	70	no
Ardeidae						
Goliath Heron	<i>Ardea goliath</i>	4450	3	27	62	no
Balaenicipididae						
Shoebill	<i>Balaeniceps rex</i>	6700	2	30	100*	no
Ciconiidae						
Oriental White Stork	<i>Ciconia boyciana</i>	5000	4	34	55	yes
European White Stork	<i>Ciconia ciconia</i> ³	3450	4	34	61	yes
Woolly-necked Stork	<i>Ciconia episcopus</i> ⁴	2200	3	31	60	no
Maguari Stork	<i>Ciconia maguari</i> ³	4200	3	31	66	no
Black Stork	<i>Ciconia nigra</i> ⁴	3000	3.5	35	67	yes
Saddlebill	<i>Ephippiorhynchus senegalensis</i>	6400	2.5	33	85	no
Marabou	<i>Leptoptilos crumeniferus</i>	7250	2.5	30	105	no
Wood Stork	<i>Mycteria americana</i>	2700	3	30	63	no
Yellow-billed Stork	<i>Mycteria ibis</i>	2400	2.5	30	55	no
Painted Stork	<i>Mycteria leucocephala</i>	3200	3.5	30	60	no

TABLE 1. Continued

Common name	Scientific name	Mass (g)	Clutch size	Incubation period (days)	Fledging period (days)	Migratory?
Bucerotidae						
Knobbed Hornbill	<i>Aceros cassidix</i>	2450	2.5	34	100	no
Great Hornbill	<i>Buceros bicornis</i>	3000	2	39	84	no
Rhinoceros Hornbill	<i>Buceros rhinoceros</i>	2700	1.5	42	79	no
Northern Ground Hornbill	<i>Bucorvus abyssinicus</i>	4000	2	39	85	no
Southern Ground Hornbill	<i>Bucorvus leadbeateri</i>	4800	2	40	86	no
Wreathed Hornbill	<i>Rhyticeros undulatus</i>	2150	2	40	90	no
Accipitridae						
Spanish Imperial Eagle	<i>Aquila adalberti</i> ⁵	3000	2.5	44	75	no
Wedge-tailed Eagle	<i>Aquila audax</i> ⁶	3500	2	45	87*	no
Greater Spotted Eagle	<i>Aquila clanga</i> ⁶	2700	2	43	63	yes
Eastern Imperial Eagle	<i>Aquila heliaca</i> ⁵	3400	2.5	43	69	yes
Steppe Eagle	<i>Aquila nipalensis</i> ⁷	3150	2	45	60	yes
Tawny Eagle	<i>Aquila rapax</i> ⁷	3400	2	42	81	no
Verreaux's Eagle	<i>Aquila verreauxii</i>	4600	2	45	94	no
Brown Snake Eagle	<i>Circaetus cinereus</i>	2050	1	49	105	no
Bearded Vulture	<i>Gypaetus barbatus</i>	5700	1.5	56	118*	no
African White-backed Vulture	<i>Gyps africanus</i>	5300	1	56	125	no
Indian White-backed Vulture	<i>Gyps bengalensis</i>	4750	1	45	90*	no
Cape Vulture	<i>Gyps coprotheres</i>	8200	1	55	140	no
Ruppell's Griffon	<i>Gyps rueppellii</i>	7400	1	55	150	no
White-bellied Sea Eagle	<i>Haliaeetus leucogaster</i>	2650	2	40	68	no
Steller's Sea Eagle	<i>Haliaeetus pelagicus</i> ⁸	7750	2	42	70	yes
African Fish Eagle	<i>Haliaeetus vocifer</i> ⁸	3400	2	44	70*	no
Madagascar Fish Eagle	<i>Haliaeetus vociferoides</i>	2500	2	41	120	no
Harpy Eagle	<i>Harpia harpyja</i>	7600	2	56	160*	no
Bonelli's Eagle	<i>Hieraaetus fasciatus</i>	2500	1.5	39	65	no
Grey-headed Fishing Eagle	<i>Ichthyophaga ichthyaetus</i>	2500	1.5	29	70	no
Hooded Vulture	<i>Necrosyrtes monachus</i>	2050	1	51	109.5*	no
Great Philippine Eagle	<i>Pithecophaga jefferyi</i>	4050	1	61	164.5*	no
Martial Eagle	<i>Polemaetus bellicosus</i>	4250	1	49	97.5*	no
Crowned Hawk Eagle	<i>Stephanoaetus coronatus</i>	3650	2	50	102.5*	no
Bateleur	<i>Terathopius ecaudatus</i>	2450	1	56	143.5*	no
Lappet-faced Vulture	<i>Torgos tracheliotus</i>	7500	1	55	130*	no
White-headed Vulture	<i>Trionoceps occipitalis</i>	5900	1	56	118	no

TABLE 1. Continued

Common name	Scientific name	Mass (g)	Clutch size	Incubation period (days)	Fledging period (days)	Migratory?
Cathartidae						
American Black Vulture	<i>Coragyps atratus</i>	2150	2	42	90	no
California Condor	<i>Gymnogyps californicus</i>	10 100	1	58	180*	no
King Vulture	<i>Sarcoramphus papa</i>	3400	1	56	90*	no
Andean condor	<i>Vultur gryphus</i>	12 500	1	59	180*	no
Sagittariidae						
Secretary bird	<i>Sagittarius serpentarius</i>	3800	2	44	86	no
Gaviidae						
Black-thorated Diver	<i>Gavia arctica</i>	3350	2	29	63	yes
Great Northern Diver	<i>Gavia immer</i>	4150	2	25	74	yes
Gruidae						
Blue Crane	<i>Anthropoides paradisea</i> ⁹	5650	2	32	85	no
Demoiselle Crane	<i>Anthropoides virgo</i> ⁹	2300	2	28	60	yes
Black-crowned Crane	<i>Balerica pavonina</i>	3600	2.5	30	80	no
Grey-crowned Crane	<i>Balerica regulorum</i>	3750	2.5	30	78	no
Wattled Crane	<i>Buggeranus carunculatus</i>	8150	1.5	35	110	no
Whooping Crane	<i>Grus americana</i>	5850	2	30	85	yes
Sarus Crane	<i>Grus antigone</i> ¹⁰	8850	2	33	93	no
Eurasian Crane	<i>Grus grus</i>	5500	2	30	68	yes
Siberian Crane	<i>Grus leucogeranus</i> ¹⁰	6400	2	29	73	yes
Hooded Crane	<i>Grus monacha</i>	3950	2	29	75	yes
Black Necked Crane	<i>Grus nigricollis</i>	6000	2	32	90	yes
Brolga	<i>Grus rubicunda</i> ¹¹	6400	2	30	100	no
White-naped Crane	<i>Grus vipio</i> ¹¹	4650	2	30	73	yes
Pelecanidae						
Australian Pelican	<i>Pelecanus conspicillatus</i> ¹²	5000	2	34	90	no
Dalmatian Pelican	<i>Pelecanus crispus</i> ¹³	9000	2	32	107*	yes
American White Pelican	<i>Pelecanus erythrorhynchos</i> ¹²	7000	2	29	80*	yes
Brown Pelican	<i>Pelecanus occidentalis</i>	3700	3	29	75	no
Great White Pelican	<i>Pelecanus onocrotelus</i> ¹⁴	11 000	2	33	70	yes
Spot-billed Pelican	<i>Pelecanus philippensis</i> ¹³	5000	3.5	30	120	no
Pink-backed Pelican	<i>Pelecanus rufescens</i> ¹⁴	5200	2	30	105*	no
Phalacrocoracidae						
European Shag	<i>Phalacrocorax aristotelis</i>	2000	3	31	53*	no
South Georgian Shag	<i>Phalacrocorax georgianus</i>	2900	2.5	30	65	no

TABLE 1. Continued

Common name	Scientific name	Mass (g)	Clutch size	Incubation period (days)	Fledging period (days)	Migratory?
Crozet Shag	<i>Phalacrocorax melanogenis</i>	2200	2.5	30	56.5*	no
Pied Cormorant	<i>Phalacrocorax varius</i>	2200	3	29	54	no
Sulidae						
Northern Gannet	<i>Sula bassama</i>	3050	1	44	90	yes
Cape Gannet	<i>Sula capensis</i> ¹⁵	2700	1	44	97	yes
Masked Booby	<i>Sula dactylard</i> ¹⁵	2100	2	44	120*	no
Blue-footed Booby	<i>Sula nebouxii</i> ¹⁶	2000	2	41	102*	no
Australasian Gannet	<i>Sula serrator</i> ¹⁶	2350	1	44	102	yes
Phoenicopteridae						
Chilean Flamingo	<i>Phoenicopus chilensis</i>	2300	1	29	75	yes
Greater Flamingo	<i>Phoenicopus ruber</i>	3550	1	29	78	yes
Diomedeidae						
Amsterdam Albatross	<i>Diomedea amsterdamensis</i>	6250	1	79	235	no
Buller's Albatross	<i>Diomedea bulleri</i>	2750	1	72	145	no
Shy Albatross	<i>Diomedea cauta</i>	4100	1	72	120	no
Grey-headed Albatross	<i>Diomedea chrysostoma</i>	3750	1	72	141	no
Royal Albatross	<i>Diomedea epomophora</i>	8200	1	79	240	no
Wandering Albatross	<i>Diomedea exulans</i>	8400	1	78	278	no
Laysan Albatross	<i>Diomedea immutabilis</i>	3250	1	65	165	no
Waved Albatross	<i>Diomedea irrorata</i>	3750	1	60	167	no
Black-browed Albatross	<i>Diomedea melanophris</i>	3900	1	71	120	no
Black-footed Albatross	<i>Diomedea nigripes</i>	3150	1	65	140	no
Sooty Albatross	<i>Diomedea fusca</i>	2500	1	70	160	no
Light-mantled Albatross	<i>Phoebastria palpebrata</i>	2800	1	69	156	no
Procellariidae						
Southern Giant Petrel	<i>Macronectes giganteus</i>	5200	1	61	118	no
Northern Giant Petrel	<i>Macronectes halli</i>	4000	1	60	113	no
Strigidae						
Pharaoh Eagle-Owl	<i>Bubo ascalaphus</i>	2300	2	34	61	no
Eurasian Eagle-Owl	<i>Bubo bubo</i>	3000	3	35	49	no
Verreaux's Eagle-Owl	<i>Bubo lacetus</i>	2600	1.5	36	63	no
Snowy Owl	<i>Nyctea scandiaca</i>	2300	7.5	32	50	no
Pel's Fishing-Owl	<i>Scotopelia peli</i>	2200	1.5	33	69	no

* Species with a significant period of postfledging care. This period was added to the fledging period for *Plecanus* only, to make the migrant-resident comparisons conservative.

Starck 1998a, Starck and Ricklefs 1998). Although this problem can be dealt with using a phylogenetic correction, such as independent contrasts (Felsenstein 1985), we avoided using this method for several reasons: first, a complete phylogeny of all relevant taxa is unavailable; and second, the high lability of developmental times could seriously impair the results of such corrections (Felsenstein 1985, Gittleman et al. 1996, Cunningham et al. 1998, Losos and Glor 2003). As we show below, developmental periods are highly variable even between closely related species.

We used two separate analyses to control for phylogenetic differences in developmental periods between distantly related taxa. We thus avoided inflating the number of degrees of freedom without sacrificing too much data. We first compared the residuals of a regression of developmental periods on body mass of migrants and nonmigrants within orders and also within families in which some species migrate while others do not. Because most of the variation in incubation periods resides at these levels (Starck and Ricklefs 1998) it is reasonable to assume that this method removes most of the phylogeny effect related to developmental strategies (Ricklefs and Starck 1998b).

We also applied a conservative method proposed by Felsenstein (1985), and paired species of large, closely related birds in which one member migrates while the other does not. We chose taxa for this comparison primarily from estimates of their phylogenetic relationships (Ricklefs and Starck 1996). If a phylogenetic hypothesis was lacking, or either all migrants or all sedentary species formed a monophyletic clade, we ranked migrant and nonmigrant congeners separately by mass, and compared pairs of equal rank. We used the phylogeny of Donne-Goussé et al. (2002) for Anserinae (with *Branta* as sister group for *Anas*), Mooers et al. (1999) for Gruinae, Roulin and Wink (2004) for Accipitridae, and Slikas (1997) for Ciconiidae. We ran a Wilcoxon signed-ranks paired test (Sokal and Rohlf 1995) in order to determine whether migrants develop faster than nonmigrants.

In addition, we analyzed all species of birds in our sample, including members of orders in which all species have a uniform pattern of migration. We used an ANCOVA (Sokal and Rohlf 1995), with body mass as the covariate, in order to compare development time of migratory and

nonmigratory species. Although this approach ignores the effects of phylogeny, we believe that the use of all species added an aspect lacking in the other methods described above: we were interested not only in relative developmental periods of closely related taxa, but also in absolute values. These are biologically distinct questions (Smith 1994): with this analysis we asked whether migrants can possess a developmental period as long as that of the slowest-developing sedentary species, regardless of phylogenetic affinity. All statistical tests were run using STATISTICA 6 (StatSoft 2003).

RESULTS

Our analyses indicated that sedentary species probably tend to lay larger clutches than do migratory ones in the same families ($F_{1,68} = 3.2$, $P = 0.08$; Table 1). The variation in clutch size between families ($F_{5,68} = 46.8$, $P < 0.001$) and the significant interaction between factors ($F_{5,68} = 6.8$, $P < 0.001$) prevented an unequivocal conclusion on the influence of migratory behavior on clutch size.

Comparing the residuals of a regression of developmental periods on body size in migrants and nonmigrants within orders and families in which both modes exist, reveals that migrants indeed develop faster (orders: $F_{1,81} = 9.8$, $P = 0.002$; families: $F_{1,68} = 9.1$, $P = 0.004$). Ordinal or familial affinity in itself did not affect the residuals (orders: $F_{4,81} = 2.0$, $P = 0.10$; families: $F_{5,68} = 1.5$, $P = 0.21$). An interaction with migratory status was apparent in both cases (orders: $F_{4,81} = 4.3$, $P = 0.003$; families: $F_{5,68} = 2.3$, $P = 0.05$). Analyzing the residuals of incubation and fledging times within families containing both migrants and resident species revealed that incubation periods did not differ between migrants and nonmigrants ($F_{1,68} = 1.1$, $P = 0.30$), but that migrants fledged faster ($F_{1,68} = 11.8$, $P = 0.001$). Familial affinity did not influence the residuals of either incubation ($F_{5,68} = 0.6$, $P = 0.69$) or fledging ($F_{5,68} = 1.5$, $P = 0.19$) times. There were no interactions with family (incubation $F_{5,68} = 1.7$, $P = 0.16$; fledging $F_{5,68} = 2.1$, $P = 0.08$).

ANCOVA showed that large migrants develop faster than large sedentary birds. This was true whether we used all large species ($F_{1,117} = 30.7$, $P < 0.001$), or only species from orders ($F_{1,88} = 26.6$, $P < 0.001$) and families ($F_{1,77} =$

25.4, $P < 0.001$) in which there are both migrants and sedentary species.

In pairs of large closely related species, migrants develop faster (Wilcoxon signed-ranks test, $n = 16$ pairs, $T = 9$, $P = 0.002$). This is achieved through faster fledging ($T = 3$, $P = 0.002$), whereas incubation periods did not differ ($T = 49.5$, $P = 0.55$).

DISCUSSION

Our results show that large migratory birds complete their development faster than do similar sized, closely related nonmigrants, and also tend to have smaller clutches. We suggest that the difference between the patterns for migratory and sedentary birds results from the selective pressure on large migrants to complete their development before the fall migration commences.

The longest development time we found for a migrant was 171 days for the Mute Swan, one of the largest of all migrants. Longer developmental periods may not enable juveniles of migrant species to complete their growth before fall migration commences. This might be the reason why no migrant birds are larger than the present-day *Cygnus*, whereas Palmqvist and Vizcaíno (2003) deduced that the 80-kg teratorn *Argentavis magnificens* had an extremely long development, and must have been sedentary in habits.

A longer developmental period may enhance the probability of juvenile survival (Ricklefs 1992, Martin 1996). If migrants have shorter developmental periods, this can be seen as incurring an additional cost for them, on top of lower annual fecundity (Böhning-Gaese et al. 2000) and survival (Cox 1985).

Another possible explanation for the shorter developmental periods of migrants is that during the breeding season at high latitude, migrants are able to obtain more resources due to high food availability and longer foraging hours in comparison with the more equatorial breeders (Cox 1985, Safriel 1995). Most migrants in our sample breed in high latitudes, whereas most sedentary species breed in more equatorial ones. Therefore the pattern we describe may result from differences in the amount of food available for low vs. high-latitude breeding birds. Hence it is possible that migrant (high latitude) species are not forced to shorten their developmental periods, but rather that sedentary (low latitude) species may be constrained by the relative scar-

city of food. Geffen and Yom-Tov (2000) found no differences in developmental periods of tropical vs. temperate passerines. It is not clear if this situation is different for other orders.

An interesting question that remains to be answered is whether migration distance affects development time. Species with long migration routes may have to accelerate their development relative to closely related species that are short-range migrants. Similarly, species migrating from high latitudes might be predicted to have shorter development than closely related species migrating from lower latitudes. We do not, at present, have sufficient data to explore this question, but the three following examples indicate the probable validity of this prediction. The Tundra Swan, migrating from the highest latitudes and covering the greatest distance of all migratory swans, has the shortest developmental period of all its congeners. In migratory geese, species migrating over long distances (Snow Goose, White-fronted Goose, Bean Goose) seem to have developmental periods over 15% shorter than those of species migrating short distances (Bar-headed Goose, Pink-footed Goose, Emperor Goose), although the Pink-footed Goose and Emperor Goose also breed at very high latitudes (del Hoyo et al. 1992). The Black-necked Crane (*Grus nigricollis*), the slowest developer among migratory species of its genus, migrates between high and low altitudes in the Himalaya region (del Hoyo 1992), whereas other cranes often undergo very long migrations. Clearly these patterns deserve further investigation.

In conclusion, we suggest that the shorter incubation and fledging periods of large-bodied migrants are a result of constraints imposed upon them by onset of fall migration. The length of summer at high latitudes may limit the length of the developmental periods of birds breeding there, and thus the size of migratory birds breeding in these regions.

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