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WHAT GROUNDS SOME BIRDS FOR LIFE? MOVEMENT AND DIVING IN THE SEXUALLY DIMORPHIC GALÁPAGOS CORMORANT

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Abstract. Flightlessness in previously volant birds is taxonomically widespread and thought to occur when the costs of having a functional flight apparatus outweigh the benefits. Loss of the ability to fly relaxes body mass constraints which can be particularly advantageous in divers, because underwater performance correlates with mass. The Galápagos Cormorant *Phalacrocorax harrisi* is flightless and the largest of its 27-member genus. Here, the loss of flight, and consequent reduced foraging range, could be compensated by enhanced dive performance. Over three years, 46 Galápagos Cormorants were successfully equipped with time–depth–temperature recorders, and 30 birds with GPS recorders during the breeding season. Birds foraged at a mean of 690 m from the nest and just 230 m from the nearest coast, confirming an extremely limited foraging range during the breeding season and corresponding increased potential for intraspecific competition. Although the maximum recorded dive depth of 73 m tallied with the species body mass, >90% of dives were conducted in water <15 m deep. The heavier males foraged in different areas and dived longer and deeper than females, which exposed males to colder water. Consideration of how plumage insulation decreases with depth indicates that diving males should lose 30% more heat than females, although this may be partially compensated by their lower surface area : volume ratio. A simple model highlights how energy expenditure from swimming underwater due to buoyancy and energy lost as heat have opposing trends with increasing depth, leading to the prediction of an optimum foraging depth defined by the volume of plumage air and water temperature. This has ramifications for all diving seabirds. It is proposed that the reduction in wing size, together with energy-expensive flight musculature, allows the Galápagos Cormorant to be more efficient at shallow depths than other seabirds, but only in warm equatorial waters. The high prey density and predictability of benthic prey in defined areas of the Galápagos can be particularly well exploited by this flightless species, with its limited foraging range, but the Galápagos Cormorant is unlikely to be able to accommodate much change in environmental conditions.

Key words: diving; Galápagos; Galápagos Cormorant; Phalacrocorax harrisi; *sexual differences; thermal constraints.*

INTRODUCTION

The supposed driver for the initial evolution of flight in birds was an enhanced ability to escape from predators (Roff 1994, McCall et al. 1998, Bennet and Owens 2002). The ability to fly increasingly enabled birds to move rapidly and efficiently over difficult terrain so that flight is now an integral part of many foraging and provisioning strategies, allowing birds access to areas and food types that could otherwise not be exploited (Jouventin and Weimerskirch 1990). However, the morphological characteristics necessary for flight are sometimes at odds with particular environments and lifestyles so that a number of previously flighted species have secondarily lost the ability to fly as they became more specialized to such conditions. Examples of this are some rails (Rallidae) that live in densely vegetated areas (Diamond 1991, Trewick 1997), where the limited advantages of flight are presumably outweighed by the costs associated with having effective wings (McNab 1994). Despite this, a primary factor in maintaining the ability to fly in many bird species still appears to be escape from terrestrial predators. New Zealand's avifauna is a prime example of this (Duncan and Blackburn 2004).

The Galápagos Cormorant *Phalacrocorax harrisi* is the only species of its 27-species genus (Johnsgard 1993) that cannot fly (Livezey 1992), presumably because it evolved on an archipelago where terrestrial predators were absent. Flightlessness is taxonomically widespread

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(McCall et al. 1998), and there are two other seabird families with flightless members: the penguins (Spheniscidae) and the steamer ducks (Anatidae). All members of the penguin family are flightless and are believed to have lost the ability to fly, although their evolution of narrow, flipper-like wings provides a mechanism much better suited for underwater propulsion than wings primarily suitable for flight (Cubo and Casinos 1997). A recently extinct member of the auk family was flightless (the Great Auk *Alca impennis*), apparently for the same reason (Livezey 1988), and the three species of flightless steamer ducks (*Tachyeres*; Humphrey and Livezey 1982, Livezey and Humphrey 1986) may also use reduced wings to help movement underwater (Livezey and Humphrey 1984). It is notable that all these flightless species are exceptionally heavy compared to volant equivalents. Great mass is enormously disadvantageous for flying birds (Jehl 1997, Hedenstrom 2002, Alexander 2005, Macleod et al. 2005) but confers distinct advantages on diving species since more massive animals can dive deeper and for longer (Schreer and Kovacs 1997, Watanuki and Burger 1999, Schreer et al. 2001, Halsey et al. 2006). Diving birds primarily use either their wings or their feet for underwater propulsion (Lovvorn and Liggins 2002). However, wings used for propulsion in both air and water cannot be efficient in either medium (Lovvorn and Jones 1994, Lovvorn et al. 1999) as studies on auks and diving petrels attest (Pennycuick 1982, 1987). In most cormorants, however, the wings are used solely for propulsion in air and the feet are used underwater (Ribak et al. 2005*a*) so that an inefficient compromise apparently need not be reached in birds of this genus (cf. Sato et al. 2006). Indeed, work on the diving capacities of cormorants (Kato et al. 2001, Gremillet et al. 2004, Ribak et al. 2004) shows them to be highly efficient, with some species reaching speeds in excess of 3 m/s underwater (Wilson and Wilson 1988), engaging in dives to depths greater than 100 m (Croxall et al. 1991) that may last over 300 s (Quintana et al. 2007). The use of wings for flight and legs for propulsion thus allows many species of cormorants to forage effectively underwater at depth and at substantial distances from their breeding sites. This theoretically allows them to exploit a large operational volume of water from their breeding sites (Wilson et al. 1992), which should reduce intraspecific competition (Birt et al. 1987).

It thus seems extraordinary that the Galápagos Cormorant has secondarily lost the power of flight. This would augur either that the lack of terrestrial predators is still the primary factor for species to maintain their powers of flight or that the increase in mass that can accompany flightlessness (Galápagos Cormorants may be more than twice the mass of any other cormorant species) results in greater benefits due to enhanced diving capacity (Schreer et al. 2001) than the substantial losses in potential foraging range. In the latter case, the diving capabilities of the Galápagos Cormorant are therefore expected to be considerably greater than those of volant species.

We examined the foraging behavior of breeding Galápagos Cormorants over three years at a variety of different sites using animal-attached temperature–depth recorders and GPS loggers. We aimed to determine the extent to which the foraging range of this species is compromised by the flightless condition and whether Galápagos Cormorants possess remarkable diving abilities which might compensate for this. We compare our findings with what is known about the foraging of other cormorant species before considering how increased body mass might benefit a species exploiting the particular marine conditions around the Galápagos Archipelago.

MATERIALS AND METHODS

Colony characteristics

A "colony" was defined as an agglomeration of one or more nests where the maximum inter-nest distance did not exceed 250 m. GPS fixes of colonies were taken with Global Positioning System (GPS-12CX-Garmin; Olathe, Kansas, USA) devices during the annual census of cormorants in September 2005 (Vargas et al. 2005). Minimum straight distances from the nest and from the coastline were calculated using ArcGIS 9 (ESRI, Redlands, California, USA).

Attached devices

Between 21 August 2003 and 17 August 2005, 95 Galápagos Cormorants were caught from a total of 18 sites (Table 1, Fig. 1) as they attended nests in the Galápagos Archipelago. Birds were caught with a hook attached to a 3-m bamboo pole and weighed to the nearest 50 g using a handheld 5-kg spring scale (Pesola, Baar, Switzerland) before being sexed. Sexes were either decided by comparison of both birds in a pair or by body mass (their most dimorphic trait, as males are significantly larger than females [Valle 1994]), or they were ascertained by taking blood samples which were used to verify gender later in the laboratory (Travis et al. 2006). Following weighing, birds were restrained and equipped with either time–depth recorders (56 birds; PreciTD, Earth and Ocean Technologies, Kiel, Germany [Daunt et al. 2003]) or GPS loggers (38 birds; Earth and Ocean Technologies [cf. Ryan et al. 2004]). Devices were taped either on the top of the middle four tail feathers (PreciTD) or on the dorsal midline feathers of the back (GPS; Wilson et al. 1997). The time–depth recorders and GPS loggers measured 19 × 75 mm (mass 20 g) and 39 × 96 mm (mass 75 g), diameter and length, respectively, and were streamlined anteriorly to reduce drag during underwater swimming. The GPS loggers that we used are considered to have a positional accuracy of better than 5 m (Ryan et al. 2004). In addition to measuring depth (to an absolute accuracy of better than 0.3 m [relative accuracy 0.1 m]), the time–depth recorders also logged temperature (to an absolute

TABLE 1. Details of the successful deployments of devices on Galápagos Cormorants during 2003, 2004, and 2005.

Nest location	Deployment date	Bird no.	Sex	Mass (kg)	Eggs	Chicks	Deployments		No. dives	No. fixes
							GPS	Depth		
Base Sur	4/8/2004	33	M	3.9	3	0		yes	65	···
Base Sur	4/8/2004	34	M	3.65	2	0	yes		···	22
Base Sur	4/8/2004	35	F	3.1	3	0	yes		···	19
Base Sur	12/12/2004	66	M	4.05	0	1	yes	yes	384	16
Base Sur	12/12/2004	67	F	···	0	1	yes	yes	229	94
Base Sur	1/14/2005	72	M	4.1	2	0		yes	323	···
Base Sur	2/27/2005	77	F	2.95	0	2	yes	yes	356	31
Base Sur	2/28/2005	78	M	3.9	0	2	yes		···	96
Cabo Douglas	8/25/2003	10	M	4.05	3	0		yes	279	···
Cabo Douglas	10/2/2003	22	F	2.8	0	1		yes	312	···
Cabo Douglas	10/2/2003	23	M	4.3	0	1		yes	318	···
Cabo Douglas	7/22/2005	92	F	3.1	0	2	yes		···	64
Cabo Douglas	7/22/2005	93	M	3.75	0	2	yes		···	118
Cabo Hammond	10/4/2004	63	M	3.8	1	1		yes	236	···
Cabo Hammond	10/4/2004	64	F	2.7	1	1		yes	845	···
Cabo Hammond	8/7/2005	94	M	3.55	0	1	yes		···	134
Cabo Hammond	8/7/2005	95	F	2.95	0	1	yes		···	45
Cañones Norte	9/27/2003	18	F	2.9	0	1		yes	578	···
Cañones Norte	9/27/2003	19	F	3.25	0	2		yes	136	···
Cañones Norte	10/6/2003	24	F	3.05	0	2		yes	1398	···
Cañones Norte	10/6/2003	25	M	3.55	0	2		yes	615	···
Cañones Norte	4/5/2004	28	M	3.8	2	0	yes	yes	219	22
Cañones Norte	4/6/2004	31	F	3	2	1	yes		···	119
Cañones Sur	8/23/2003	5	F	2.65	3	0		yes	72	···
Cañones Sur	8/23/2003	6	M	3.55	2	0		yes	140	···
Cañones Sur	4/9/2004	37	M	3.5	3	0		yes	214	···
Cañones Sur	10/1/2004	61	F	2.85	2	1		yes	362	···
Carlos Valle	8/24/2003	7	M	4.1	0	1		yes	122	···
Carlos Valle	8/24/2003	8	F	2.8	0	1		yes	134	···
Carlos Valle	9/7/2003	12	M	3.75	0	1	yes		···	2059
Carlos Valle	5/11/2004	44	F	2.6	0	1	yes		···	461
Carlos Valle	5/11/2004	45	M	3.55	0	1	yes		···	1598
Carlos Valle	5/11/2004	46	M	3.6	0	1	yes		···	602
Carlos Valle	12/15/2004	71	M	4	0	1	yes	yes	253	1882
Colonia Escondida	4/10/2004	38	M	3.2	2	0	yes		···	6
Colonia Escondida	4/10/2004	39	F	2.85	2	0	yes		···	2494
Colonia Escondida	4/10/2004	40	M	3.85	2	0		yes	159	···
Elizabeth Norte	8/22/2003	3	F	2.5	0	1		yes	161	···
Elizabeth Norte	9/20/2003	13	F	2.95	2	0	yes		···	1469
Espinosa Sur	9/24/2003	16	M	3.65	3	0	yes	yes	100	···
Espinosa Sur	9/24/2003	17	F	2.8	3	0		yes	318	···
Espinosa Sur	4/12/2004	41	F	···	3	0	yes		···	486
Espinosa Sur	4/12/2004	42	M	···	3	0	yes		···	239
Hector Serrano	9/30/2003	20	F	2.45	1	1		yes	352	···
Hector Serrano	9/30/2003	21	M	3.8	0	1		yes	557	···
Hector Serrano	4/1/2004	26	F	3.1	2	0	yes	yes	425	478
Hector Serrano	4/3/2004	29	M	3.6	0	1		yes	370	···
Hector Serrano	9/28/2004	54	F	2.7	0	1		yes	449	···
Hector Serrano	9/28/2004	55	M	3.7	0	1		yes	492	···
Hector Serrano	9/28/2004	57	F	2.5	0	1		yes	217	···
Pargos	6/26/2005	87	F	2.65	0	2	yes		···	469
Pargos	6/26/2005	88	M	4.1	0	2	yes		···	518
Playa de los Perros	2/16/2005	75	F	2.75	3	0	yes		···	15 294†
Playa de los Perros	2/17/2005	76	F	2.5	3	0	yes		···	16 577†
Priscilla Sur	9/22/2003	14	F	2.75	0	2		yes	175	···
Priscilla Sur	9/22/2003	15	M	4.1	0	2	yes	yes	51	36 786†
Priscilla Sur	4/1/2005	86	F	2.75	1	1	yes		···	576
Punta Moreno	8/21/2003	1	M	4.1	0	1	yes	yes	245	···
Punta Moreno	8/21/2003	2	F	···	0	2		yes	147	···
Rocas Pinguino Sur	4/12/2004	43	M	···	2	0	yes		···	118
Rocas Pinguino Sur	3/2/2005	81	F	2.5	0	2	yes		···	219

Notes: Localities are shown in Fig. 1. Blank cells indicate that the treatment was not applied. Ellipses indicate that data were not available.

† Data obtained from birds while close to the nest (and possibly on it) rather than just at sea where geo-referencing data from the locality did not allow us to differentiate sea from land periods.

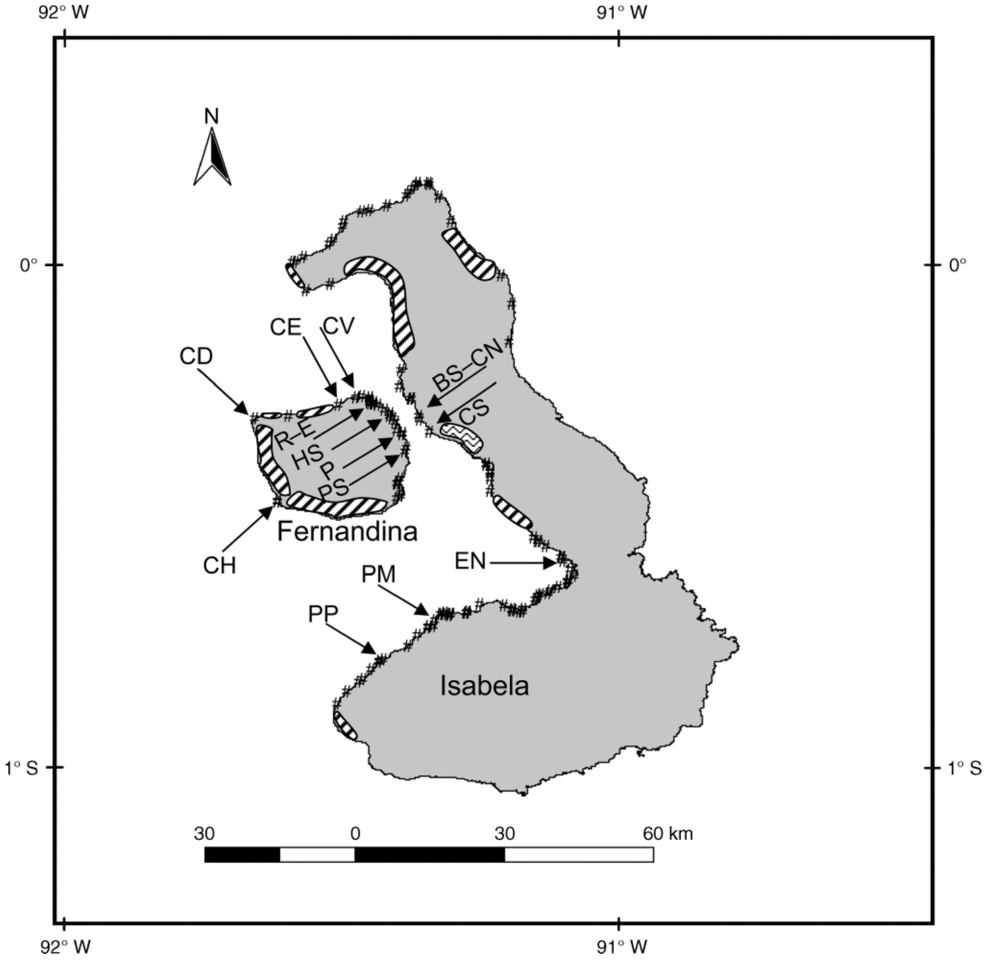

FIG. 1. Map showing distribution of Galápagos Cormorant colonies in 2005 ("#" symbols). Arrows indicate location of sites where devices were successfully deployed between 2003 and 2005: CD, Cabo Douglas; CH, Cabo Hammond; PS, Priscilla Sur; P, Pargos; HS, Hector Serrano; R, Rocas Pinguino Sur; E, Espinosa Sur; CV, Carlos Valle; CE, Colonia Escondina; BS, Base Sur; CN, Cañones Norte; CS, Cañones Sur; EN, Elizabeth Norte; PM, Punta Moreno; PP, Playa de los Perros (cf. Table 1). The hatched sections on Fernandina and Isabela (southern, western, and northeastern) are cliffs, and the zigzag patch on Isabela indicates particularly heavy swells leading to rough seas, both of which are presumed to prohibit land access by cormorants.

accuracy of better than 0.1°C) from a rapid external sensor located on the end of a protruding wire (Daunt et al. 2003) that was immersed in the water during swimming, even at the surface. Both time–depth and GPS recorders logged data in a flash random access memory and were programmed to record continuously at frequencies of either 0.5 or 1 Hz. The device attachment process took less than 30 min, after which birds were released back at the nest site. After at least one foraging trip was judged to have taken place (typically 24–48 h later), the birds were recaptured, the devices removed, and data downloaded onto a field computer.

Forty-six of the deployed temperature–depth devices yielded useful data for both temperature and depth for a period in excess of 20 minutes of diving (Table 1). However, data from only 36 of these (from 19 males and 17 females) were used for assessment of depth utilization by the cormorants because they contained data from at least two complete foraging bouts (this stipulation was added because we noted that depth use during foraging trips often showed progressive changes in depth utilization so that use of partial foraging bouts would introduce a behavioral bias). Similarly, although 38 GPS loggers were deployed on birds, data from only 30 (from 14 males and 16 females) were used (Table 1). Overall, reasons for deployments considered unsuccessful included individuals that did not dive or move within the period of being equipped, water leaking into the units, unstable baselines in the depth recordings, temperature sensors that broke off during deployment, and units that stopped recording earlier than programmed, perhaps due to knocks sustained in the housing from the birds.

Dive data were analyzed using ANDIVE (Jensen Software Systems, Laboe, Germany), a program that identifies the start and end of each dive as well as the beginning and end of the bottom phase of dives based on points of inflection in the dive profile (with the onset of the bottom phase being taken to occur nominally when the rate of change of depth was <0.1 m/s for more than two consecutive seconds, this occurring within 85% of the maximum depth reached during the dive). Using these data, the program produces an ASCII file of the following dive parameters: time of dive begin, maximum depth reached, total dive duration, descent duration, bottom duration, ascent duration, rate of change of depth (vertical speed) for the descent, bottom and ascent phases, and post-dive rest duration. These data can then be treated by standard analytical methods. We defined dives as any depth greater than twice the resolution of the logger, i.e., depth > 0.6 m.

As the distribution of most dive variables were not normal, data were log-transformed before conducting statistical tests. Following this transformation, the normality of the data was verified using an Anderson-Darling test. We also verified the equality of the variances between compared variables. Where normality and equal variance conditions did not apply, nonparametric tests were used. In order to control for potential pseudoreplication, trends were highlighted using restricted maximum likelihood analyses (REML; Patterson and Thompson 1971) with individuals as random factor and sexes computed as fixed factors. In this test, a probability < 0.05 on the interaction term (Variable × Group, e.g., Maximum depth × Sex) indicated that the slopes of the regression lines between the groups differed significantly. If the slopes were not different, the interaction term was removed from the model. Subsequently, a $P < 0.05$ on the group term (sex) indicated that the intercepts of the regressions were different. Statistical and numerical analyses were conducted using JMP version 5.1.1J (SAS Institute, Cary, North Carolina, USA), MINITAB version 14.20 (MINITAB, State College, Pennsylvania, USA), as well as in SYSTAT version 10 (SPSS, Chicago, Illinois, USA).

RESULTS

Colony characteristics

Galápagos Cormorant colonies were located primarily on the southwestern and northern sides of Isabela and on the eastern side of Fernandina Islands between 0.17° N–0.87° S and 91.19° W–91.66° W (Fig. 1). Fig. 1 also indicates cliffs and coastline exposed to rough seas where birds have no access to land from the water. Modal minimum intercolony distance between adjacent colonies was less than 1 km, with the frequency distribution of intercolony distance decreasing rapidly after that (Fig. 2a). The greatest distance between any one colony and the next closest was 24 km. "Colony" size comprised between one and 15 pairs. However, modal colony size was one during the 2005 census of the population, with the frequency of occurrence of colony size declining sharply after one (Fig. 2b).

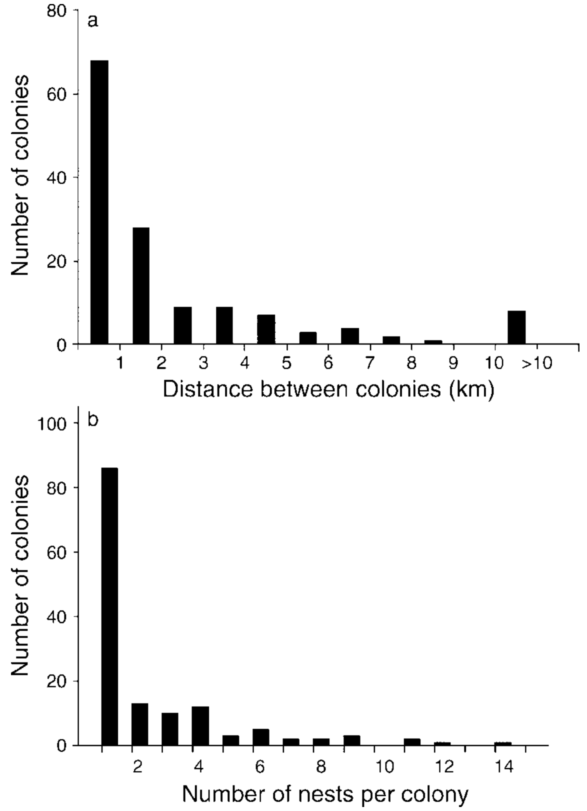

FIG. 2. (a) The frequency distribution of the minimum distances (along the coast) between adjacent Galápagos Cormorant colonies. (b) The frequency distribution of the different colony sizes of the Galápagos Cormorant.

Attached devices

Of the birds caught to be equipped with devices, body mass of males (3.77 ± 0.26 kg, mean ± SD, range 3.2–4.3 kg, $N = 44$ males) was significantly higher than that of females (2.78 ± 0.22 kg, range 2.3–3.25 kg, $N = 46$ females; $t = 19.6$, $P < 0.001$), with there being only one female heavier than the lightest male. Of the 92 devices deployed, all (100%) were recovered. A single bird abandoned its nest (containing two eggs). In that case, it was equivocal whether this was due to our procedures or whether the eggs did not hatch for another reason (see Valle [1994], who notes, "The most pervasive factor leading to clutch size reduction was the failure of eggs to hatch which occurred at 42% of the nests and accounted for 43% of egg mortality ($N = 88$ eggs lost) and 21.5% of 177 eggs laid"). Other than this, no deleterious effects of the devices were observed, and where birds were observed to return from foraging, they were also seen to feed chicks.

Movement

The movement exhibited by foraging Galápagos Cormorants was highly local and tended to be along the coast rather than out to sea (Fig. 3). No individual ranged farther than 7 km from the nest and 1 km from

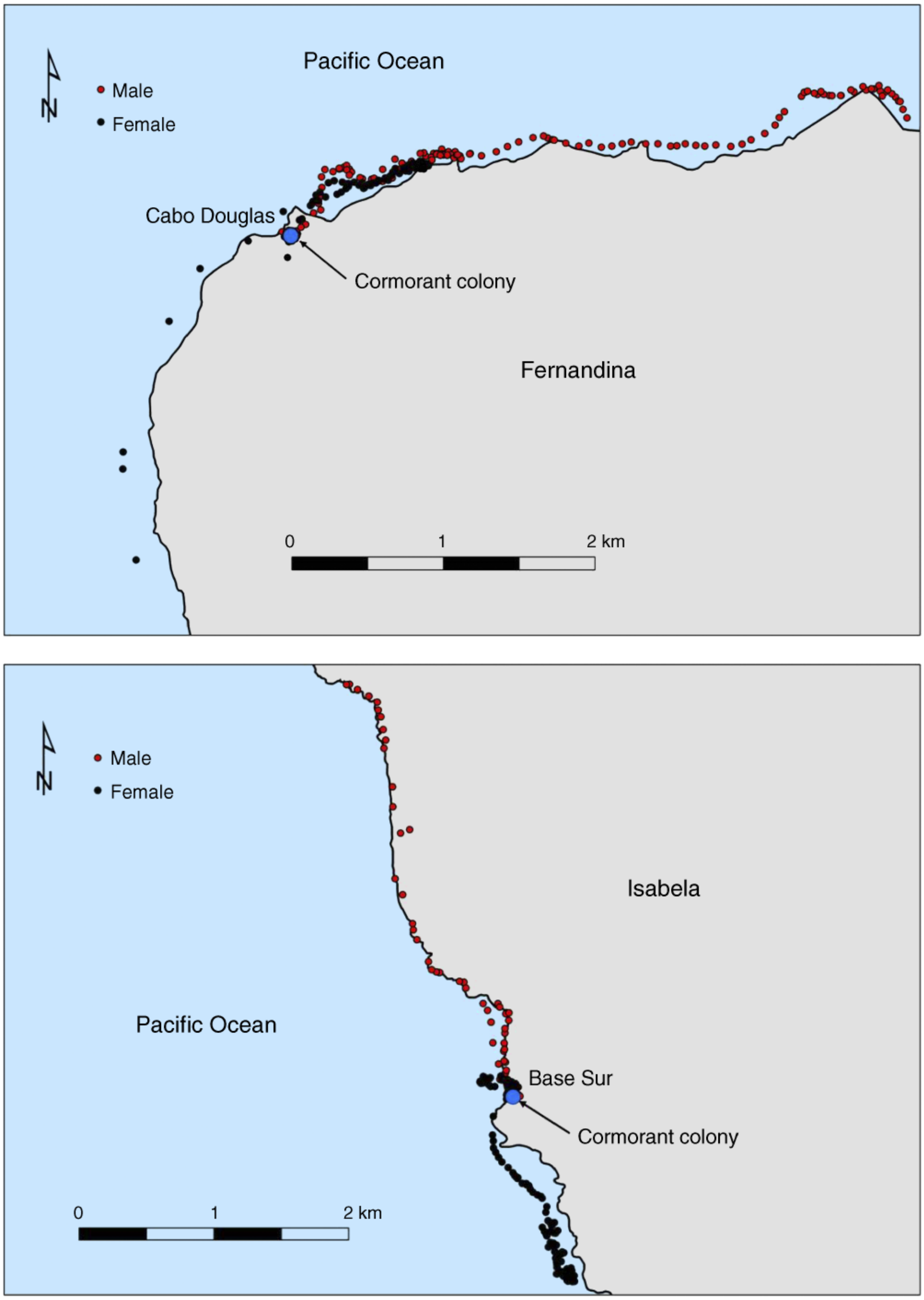

FIG. 3. Examples of movement undertaken by two male (red traces) and two female (black traces) Galápagos Cormorants, from two single pairs, at two different localities as determined by GPS loggers during foraging trips. Note how localized the movements are and the proximity of the birds to the coast. Points apparently on land are due to inaccuracies in the map of Galápagos.

the coastline (Table 2). Mean foraging distance from the nest was significantly higher in males than females ($F_{1,28} = 6959.87$, $P < 0.001$; Table 2). However, estimates of parallel distances measured from the coastline indicated that females foraged farther out to sea than males ($F_{1,28} = 550.46$, $P < 0.001$; Table 2).

Diving behavior

A total of 11 467 dives was analyzed from 36 birds (318 ± 253 dives/trip, mean ± SD). Galápagos Cormorants showed two major dive types based on the dive profile of depth vs. time: "V-shaped" dives, where birds descended at a constant rate to a particular depth before

TABLE 2. Movements of 16 female and 14 male Galápagos Cormorants equipped with GPS devices between 2003 and 2005.

			Foraging distance (km)			
Distance category	Sex	No. GPS fixes	Mean	SE	SD	Maximum
From the nest	females	54 166	0.659	0.003	0.731	5.453
	males	7370	0.892	0.014	1.202	6.356
	both sexes	61 536	0.687	0.003	0.806	6.356
From the coastline	females	9838	0.252	0.002	0.174	0.745
	males	2285	0.146	0.002	0.092	0.492
	both sexes	12 347	0.231	0.001	0.166	0.745

Note: Distances from the nest excluded fixes in a 30 m radius around the nest due to GPS and base-map errors.

returning in a similar manner directly to the surface (5% of all dives), and "U-shaped" dives (95% of all dives), where birds spent extended times swimming, presumably along the seabed, at rather specific depths (for further definition of different dives types see Schreer and Testa [1995, 1996]). A further dive type, "parabolic," where there were no points of inflection in the depth–time profile (Wilson et al. 1995), accounted for <1% of all dives.

Pooling all dive data, dive duration increased significantly with maximum depth ($F_{1,4755} = 19\,424.3$, $P < 0.001$) and the trends differed between sexes in both the slopes of the regressions (interaction term, $F_{1,4755} = 156.0$, $P < 0.001$) and the intercepts ($F_{1,8111} = 13.03$, $P < 0.001$). Durations of dives pooled across females increased with depth at a faster rate than males until ~5.5 m depth, where the situation reversed, with durations of dives pooled across males increasing at faster rates than those of females (for females, $0.45 \ln(x) + 2.78$; $R^2 = 0.60$; for males $0.54 \ln(x) + 2.63$; $R^2 = 0.71$; Fig. 4a). The descent rate from dives pooled across all birds also increased significantly with maximum depth ($F_{1,10\,170} = 8478.0$, $P < 0.001$), and here again the trends differed between sexes in both the slopes of the regressions (interaction term: $F_{1,10\,170} = 128.5$, $P < 0.001$) and the intercepts ($F_{1,10\,180} = 43.2$, $P < 0.001$). As was the case for the dive duration, the descent rates from dives pooled across females increased with depth at a greater rate than for males until ~2.5 m before the trend reversed (for females, $0.72 \ln(x) - 1.54$; $R^2 = 0.45$; for males, $0.56 \ln(x) - 1.39$; $R^2 = 0.52$; Fig. 4b). The ascent rate, too, increased significantly with depth ($F_{1,10\,307} = 12\,624.7$, $P < 0.001$) and showed different trends between sexes in both slopes (interaction term: $F_{1,10\,307} = 17.2$, $P < 0.001$) and intercepts of the regressions ($F_{1,10\,313} = 314.0$, $P < 0.001$), but this time the ascent rates of dives pooled across females always increased with depth at a greater rate than for males (for females, $0.67 \ln(x) - 1.38$, $R^2 = 0.52$; for males, $0.63 \ln(x) - 1.47$, $R^2 = 0.57$; Fig. 4c). Finally, after excluding dives where birds spent <1 s in the bottom phase (V-shaped dives), bottom phase duration of dives pooled across all birds was found to increase significantly with dive duration ($F_{1,99\,456} = 34\,556.0$, $P < 0.001$) and although the slopes of the regressions for dives pooled across males and females were not different (interaction term: $F_{1,9456} = 1.43$, $P = 0.23$) the intercepts were (after removing the

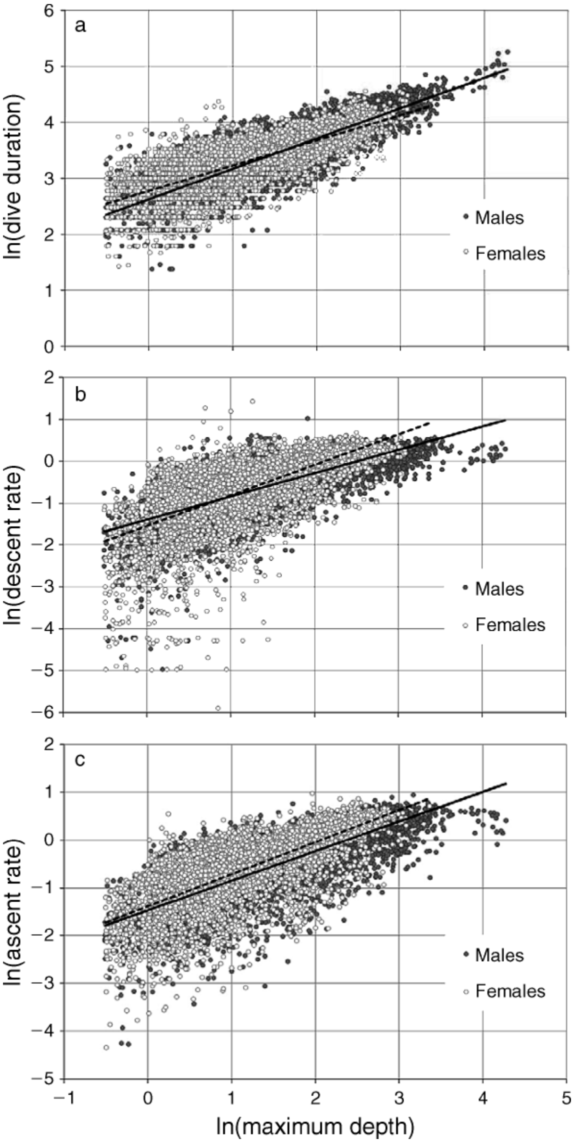

FIG. 4. Example of how (a) total dive duration (measured in seconds), (b) rate of descent (measured in m/s), and (c) rate of ascent (measured in m/s) vary with maximum depth (measured in m) reached during dives made by Galápagos Cormorants. All data have been log-transformed. The lines of best fit are: for males, solid line, darker points; and for females, dashed line, lighter points.

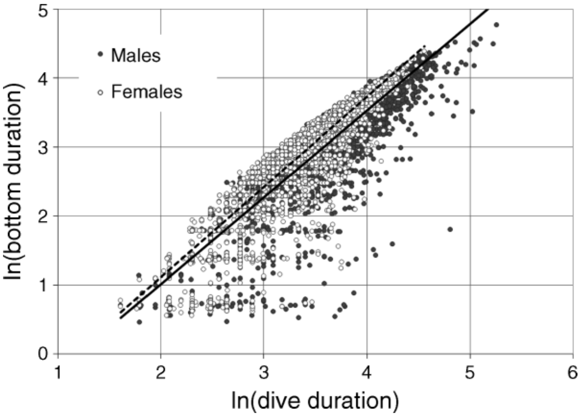

FIG. 5. Relationship between the duration of the bottom phase of dives and total dive duration for male (dark points, continuous line) and female (light points, dashed line) Galápagos Cormorants. Dive duration data, originally measured in seconds, have been log-transformed.

interaction term from the model: $F_{1,9468} = 780.9$, $P < 0.001$). Here, the duration of the bottom phase of dives pooled across females always increased with dive duration at a greater rate than males (for females, 1.31 ln(x) – 1.52; $R^2 = 0.82$; for males, 1.26 ln(x) – 1.51; $R^2 = 0.75$; Fig. 5).

On average, males dived significantly deeper (6.92 ± 6.63 m [mean ± SD], range 0.1–71.9 m; one-way ANOVA on log values: $F_{1,2274} = 690.8$, $P < 0.001$) than females (4.23 ± 3.63 m, range 0.1–28.9 m). A detailed examination of the dive-depth distribution (Fig. 6) showed that females used predominantly the shallow parts (<5 m) of the water column, while males dived predominantly in the depths categories (>5 m). Based on this result, we separated dives into deep (≥5 m) and shallow (<5 m) and compared the proportion of each category between males and females using a chi-square test. The test confirmed that females dived significantly more often than males in the 0–4 m depth range, the reverse being true for dives >5 m ($\chi^2_1 = 644.4$, $P < 0.001$).

Maximum depth reached by any bird was 73.2 m and maximum dive duration 196 s. Similarly, maximum descent, bottom, and ascent durations were 70.3, 93.5, and 82.8 s, respectively. Maximum dive duration (in seconds) by any individual bird increased significantly with maximum dive depth (in meters) according to this equation: Duration = 1.98(Depth) + 45 (where $R^2 = 0.84$, $F_{1,31} = 90.4$, $P < 0.001$). If males and females were pooled, maximum dive duration also increased significantly with body mass (in kilograms) ($N = 18$ males and 15 females of known mass) according to this equation: Duration = 16.8(Mass) + 22.6 (where $R^2 = 0.12$, $F_{1,31} = 4.51$, $P < 0.05$), although the relationship was not significant for either males or females alone. Similarly, both mean dive depth and maximum dive depth increased with body mass according to these equations: Mean depth = 2.64(Mass) − 3.2 (where $R^2 = 0.18$, $F_{1,31} = 7.72$, $P < 0.02$) and Maximum depth = 9.11(Mass) − 13.6 (where $R^2 = 0.18$, $F_{1,31} = 6.93$, $P < 0.05$), although the relationship was not significant if males or females were considered alone.

Temperature variation down the water column

Although the oceanographic conditions during the study period were fairly constant, being typified by La Niña conditions (Vargas 2006), water temperature experienced by the diving cormorants varied substantially as a function of depth, even varying considerably during the course of single foraging trips, presumably due to birds moving through different bodies of water (Fig. 7a). Water temperature also varied between sites, with sharp thermoclines representing temperature changes of 4–5°C occurring at depths between 3 and 18 m (Fig. 7b). To derive a general relationship, all temperature/depth profile data for depths <30 m (only one bird dived substantially deeper than this) were combined, thus incorporating all the biases according to site and season, to give a relationship between temperature and depth: Temp = 20.2 – 0.215(Depth) (where $R^2 = 0.79$).

Not all males and female cormorants, however, experienced the same underwater temperature regime, even after depth, time, and locality effects are corrected. Where breeding pairs of birds were equipped and foraged on the same day (a total of 12 pairs), six of the females dived in warmer water than their corresponding males for any given depth (paired t tests, $P < 0.01$) although the behavioral mechanism by which this was brought about was not clear. There was no significant difference in water temperature between males and females for the other six pairs ($P > 0.05$).

DISCUSSION

Is the Galápagos Cormorant a better diver than other congeners?

Among both reptiles and warm-blooded animals, there is extensive literature that documents increasing

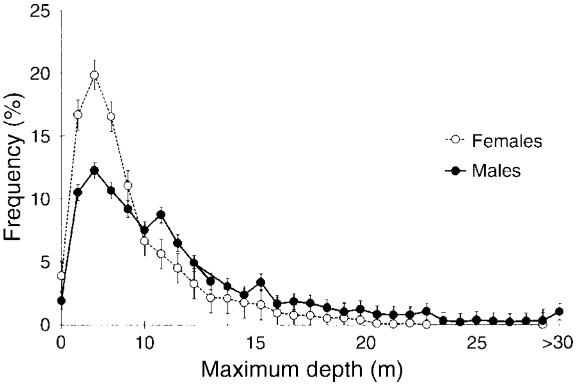

FIG. 6. Frequency distribution (mean ± SE) of the dive depth, averaged per 1-m depth increment, for male and female Galápagos Cormorants.

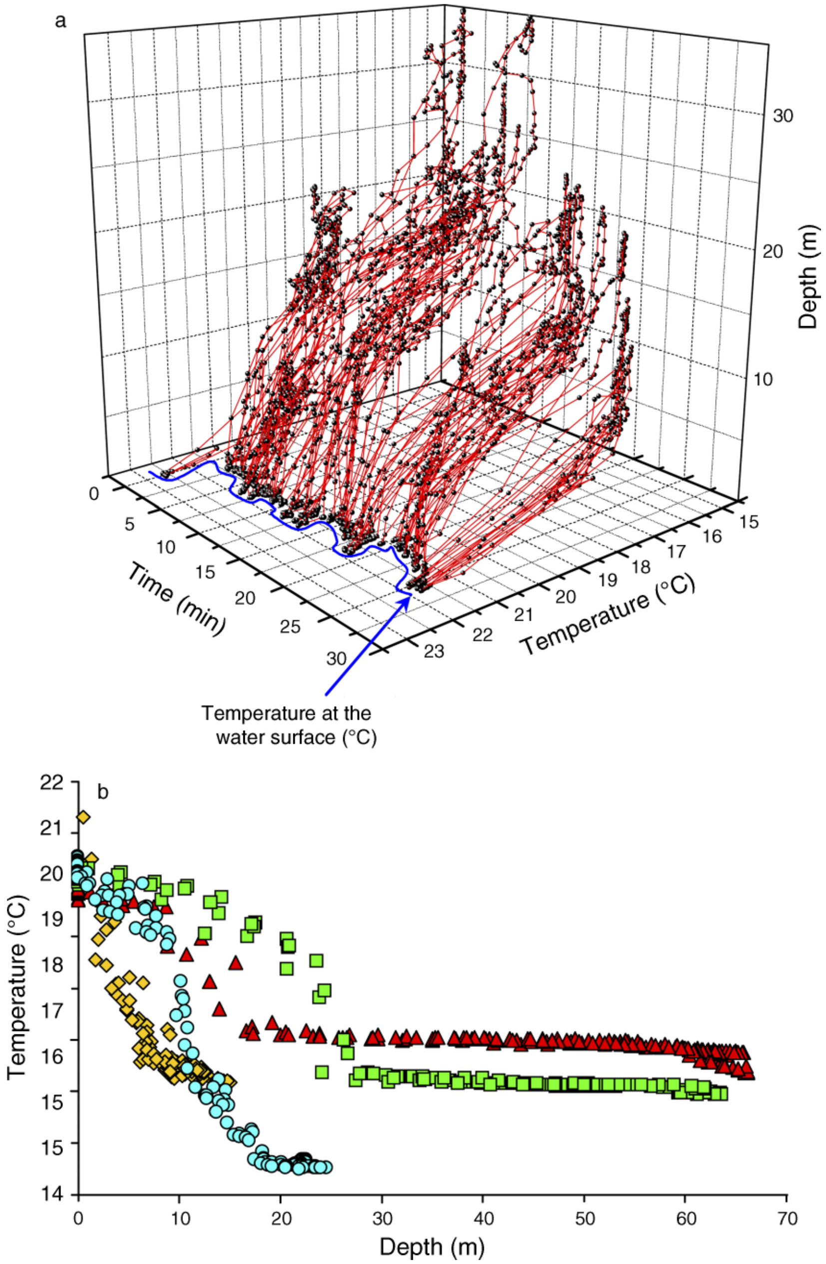

Fig. 7. (a) Changes in water temperature as a function of depth (vertical axis; increasing depth is shown higher) and locality (depicted by time since the bird was assumed to be moving during foraging) as recorded by a male Galápagos Cormorant during a foraging bout from Hector Serrano on 29 September 2004. Note that the temperature at both the water surface (see blue arrow and continuous blue track at 0 m on the plane defined by the time and temperature axes) and at depth varies substantially during the course of foraging. This is highlighted in (b), where some temperature–depth profiles derived from different birds or periods are shown: blue circles from a section of the bird in (a), red triangles and green squares for different periods of a foraging trip made by a male at Cabo Hammond on 4 October 2004, and yellow diamonds from a female foraging at the same locality on the same date.

diving capabilities with increasing body mass (Burger 1991, Schreer and Kovacs 1997, Schreer et al. 2001, Halsey et al. 2006). The ability to dive for longer, and therefore have more time for diving deeper, appears to be related, in part, to decreasing mass-specific metabolic rate with increasing mass and an oxygen storage capacity that scales linearly with body mass (Peters 1983). In essence, larger animals use their oxygen stores less quickly than do smaller ones. We hypothesized that the development of flightlessness in the Galápagos Cormorant allowed body mass to increase (but see Scott et al. [2003]), conferring advantages in terms of diving capacity. We thus expect this species to outperform its smaller congeners, all of which fly and all of which are

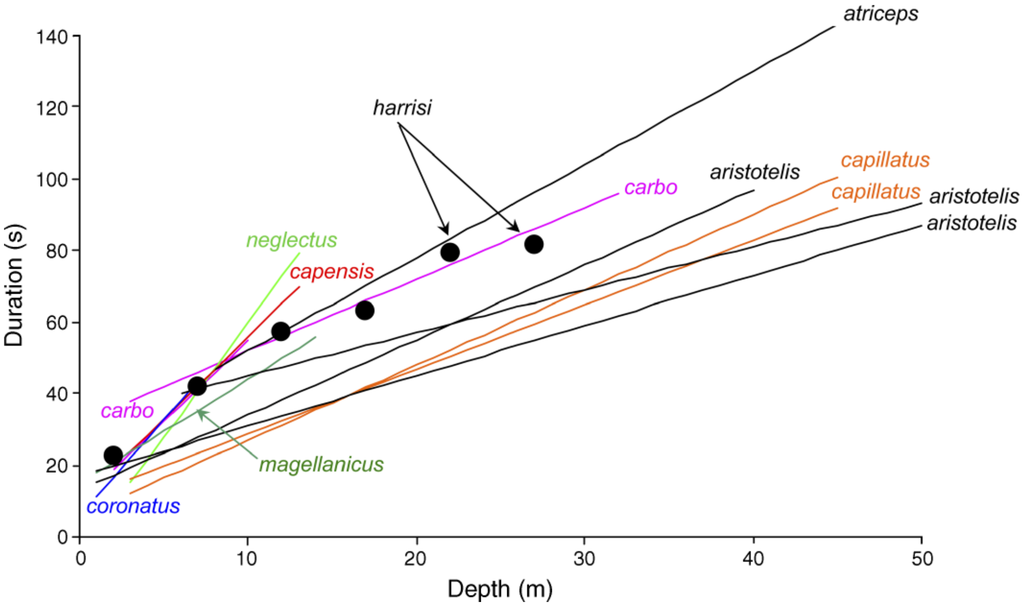

FIG. 8. Dive duration of various cormorants (*Phalacrocorax*, specific names as given in figure in italics) in relation to depth (taken from published relationships) and compared for mean duration (both male and female) vs. depth data from the Galápagos Cormorant (black circles). Where possible, the depth data have been limited to those depths actually frequented by the cormorants in the respective studies. Repetitive regression lines for *P. aristotelis*, *P. capillatus*, and *P. carbo* are taken from studies presenting results from birds foraging at different places or times of year and give some measure of intraspecific variability. The figure is adapted from Quintana et al. (2007).

lighter than the Galápagos Cormorant (Johnsgard 1993). Quintana et al. (2007) present data on both maximum dive durations and maximum dive depths vs. body mass for 23 cormorant species. Using their data, we compute that there is no apparent significant relationship between body mass (kilograms) and maximum dive depth, but that maximum dive duration (in seconds) increases with body mass according to Duration $= 3.1 + 65.4$(Mass) (where $R = 0.47$, $P < 0.01$, $N =$ 23 species; Quintana et al. 2007; Fig. 4). With a mean body mass of 3.25 kg, Galápagos Cormorants are predicted to dive for a maximum of 216 s, close to our recorded maximum of 196 s. It would thus seem that Galápagos Cormorants can indeed benefit from their large body size in that this enables them to dive for extended periods. However, such long, deep dives are exceptional, with 90% of dives terminating at depths of less than 8 and 15 m for females and males, respectively (Fig. 6), with equivalent total dive durations being less than 43 and 62 s, respectively, so the relevance, aside from the physiological interest, is questionable. We note here, though, that the study was conducted during the highly productive conditions of La Niña with likely abundant food supplies. However, the ability to dive deeper and for long periods may be crucial for survival during the poor feeding conditions typical of El Niño episodes.

Beyond simple maxima relating to depth and time underwater, duration as a function of maximum depth reflects the cormorant's response to depth, so some measure of an enhanced diving capacity might be gained by assessing how dive duration with respect to depth in Galápagos Cormorants compares to that of congeners. Data taken from a figure which summarizes this for nine species of cormorant in Quintana et al. (2007: Fig. 8) do indeed suggest that Galápagos Cormorants are consistently among the species able to stay underwater the longest for any given depth. The linear scaling of body oxygen stores in relation to mass coupled with the decelerating metabolic rate (Peters 1983) might, in part, account for this. Otherwise, there are indications that being flightless might allow divers to reduce mass-specific metabolic rate, something that would also tend to increase the time available underwater for any given depth.

Why is the Galápagos Cormorant flightless?

In consideration of the mechanisms that might have led to their evolution of flightlessness in the Galápagos Cormorant, a primary issue will relate to the costs of having functional wings (McCall et al. 1998). For example, the reduced body density in volant birds, primarily mediated by features such as pneumatized bones (Cubo and Casinos 2000), results in increased upthrust underwater, against which diving birds must expend energy by actively working, or they would float back to the surface (Lovvorn et al. 2004). Similarly, the air trapped within large wings is likely to contribute substantially to unwanted buoyancy underwater (Wilson et al. 1992). The placement of such large wings along the sides of the body, and the large pectoral muscles associated with them, presumably also increases body girth so that overall body drag, which is given by

$$\text{Drag} = 0.5(\text{Speed})^2 \times \rho \times \text{Cd} \times A \tag{1}$$

(where ρ is the body density, Cd is the drag coefficient, and A is the cross-sectional area at the point of greatest girth) also increases. Since A is proportional to the square of the radius, a small increase in bird body diameter increases the drag disproportionately more. Drag in birds is also known to be substantially dependent on vibration in the feathers (Lovvorn 2001), so a lack of the long feathers (primaries and secondaries) necessary for flight, something that is obvious in both penguins and Galápagos Cormorants, could also help reduce the energetic costs of swimming underwater (cf. Bridge [2004]).

Costs also include those of production and maintenance of a flight apparatus. The pectoral muscles, for example, may form >15% of the total body mass (Lindstrom et al. 2000, Ostnes et al. 2001, Saarela and Hohtola 2003; and here it is notable that the Galápagos Cormorant has a substantial reduction in pectoral muscle mass compared to other cormorants [Livezey 1992]), and there is a large surface area of feathers that needs particular attention (Zampiga et al. 2004, Gremillet et al. 2005*a*). Furthermore, energy expenditure during flight is comparatively high (Butler et al. 2000, Hambly et al. 2004) due to the work done by large wing muscles which, even though not actively used underwater, presumably use body oxygen stores during diving, which will tend to increase the overall metabolic rate of birds and likely compromise dive durations.

Finally, birds that dispense with flight are not subject to flight-linked restrictions on body mass and may benefit in various ways by becoming larger (Bednekoff 1996). This has advantages for diving species because animals that are more massive can dive longer and deeper (Schreer et al. 2001, Halsey et al. 2006), but it is also advantageous with respect to heat loss being less due to changes in surface area : volume ratios (cf. Bustamante et al. [2002]); see *Discussion: Flight and foraging underwater*).

Conversely, the advantages of being able to fly are, however, considerable. Aside from escape from predators, flight allows enhanced access to specific areas (e.g., safe nesting areas [Jenkins 2000]) or particular food sources (Bonadie and Bacon 2000), allows rapid movement (which allows birds to react to, and exploit, ephemeral prey [Schwemmer and Garthe 2005]), which can result in an increased foraging range (Huin 2002) and facilitated migration (Matthiopoulos et al. 2005). Aside from the predator issue, the main advantages of flight relate to efficient access to food. Given the importance of flight in food acquisition by birds, we might similarly expect that particular foraging conditions in Galápagos select for flightlessness.

Prey availability and flightlessness

Although the metabolic costs of flight (expressed in terms of mass-specific power) are generally substantially higher than those of swimming, even underwater (Peters 1983), the high speed of flight means that costs of transport, in terms of the energy spent per unit distance traveled (Alexander 2005), are lower in fliers than swimmers (Peters 1983). Thus, the overall costs of traveling between a nesting site on land and a foraging site at sea increase faster (linearly) with distance in swimmers than in fliers (Fig. 9a). Prey availability (which ultimately equates with the amount of prey that can be ingested during a specific time spent foraging) can vary in a number of ways as a function of distance from the resting site (Gremillet et al. 2004). Typically, though, we would expect it to increase with distance due to the effect of Ashmole's halo brought about by intraspecific competition (Birt et al. 1987, Forero et al. 2002; we note here that the small numbers of birds in Galápagos Cormorant colonies [Fig. 2b] would minimize this effect). Any time that prey density increases with distance in such a way that the gain during foraging is less than the total travel costs, the nesting site becomes unprofitable and therefore not tenable. However, since flight costs of transport are less than those of swimming, volant birds can exploit lower prey densities than swimming birds (Fig. 9b, distance 0.6–1.6) and this condition will hold true for any distance (Fig. 9b, distance 2–5). All other things being equal, therefore, it would initially seem that there is no situation where flightless individuals might benefit over flying counterparts. However, as discussed above, the production and maintenance of functional wings implies substantial costs which should be subtracted from the overall energetic gain for volant birds (dotted line in Fig. 9b). When these costs are high, they can result in volant birds faring less well than flightless individuals, with the condition being most apparent for short traveling distances (Fig. 9b, distance 0–0.6). Thus, flightless individuals can indeed fare better than volant conspecifics if the overall distances traveled to forage are small and if prey encounter rates are high. The data on Galápagos Cormorant movement comply with this, showing that distances ranged during foraging are typically <1 km. This contrasts starkly with data from other cormorant species, where birds may move several, and up to tens of, kilometers to feed (e.g., *P. carbo* [Gremillet et al. 1999*a*], *P. aristotelis* [Wanless et al. 1993], *P. gaimardi* [Gandini et al. 2005], *P. olivaceus* [Quintana et al. 2004], *P. atriceps*, and *P. magellanicus* [Sapoznikow and Quintana 2003]). There is also good reason to believe that the large diversity of bottom-dwelling prey on which the Galápagos Cormorant feeds (cf. Valle 1995; F. Hernán Vargas, *unpublished data*) is locally abundant (Edgar et al. 2004) as the flightless condition requires. The eastern tropical Pacific has some of the most productive waters in the world (Fiedler et al. 1991), and the confluence of currents leads to particularly high productivity around Fernandina and Isabela Islands (the only sites where the cormorants nest; Fig. 1) with a disproportionately high number of fish taxa and

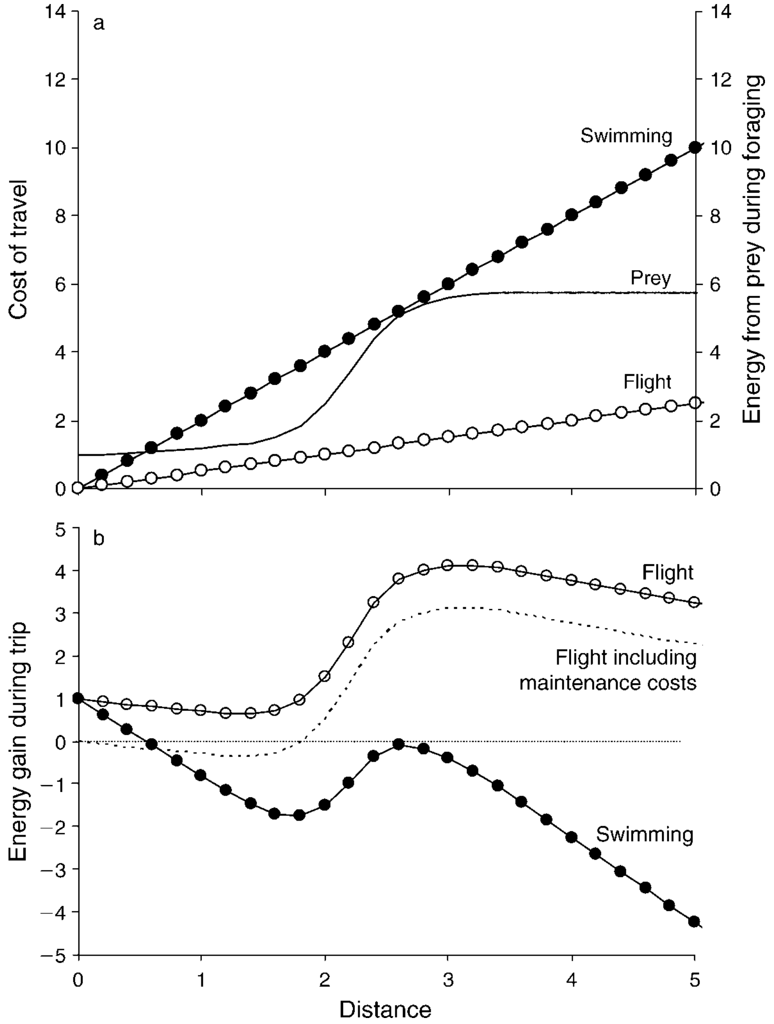

FIG. 9. (a) Overall cost of travel (lines with circles) for two different modes of locomotion for birds moving to and from a foraging area. In this example, swimming costs of transport (e.g., J/m) are taken to be four times higher than those of flight. A further single line shows a generated distribution relating to prey abundance as a function of distance from the starting spot (see *Discussion: Prey availability and flightlessness*). If, for simplicity, the time in the foraging area is considered constant, then the amount of prey taken per foraging trip (shown by the continuous line) will be linearly related to prey density. (b) A simplified output of the net energy gain during a trip according to travel mode and distance where travel costs (lines with circles in panel a) are simply subtracted from the overall energy gain during foraging (continuous line in panel a). The dotted line shows how costs of growth and maintenance of the flight apparatus, coupled with costs associated with flight-dependent inefficiency underwater, might reduce the net energy gain by flying.

elevated fish abundance (Edgar et al. 2004). Although the pelagic fish of the region support a number of seabirds (Mills 1998), the cormorant's reliance on bottom-dwelling fish means that it exploits a resource that is spatially and temporally more predictable (cf. Litzow et al. [2004]), as befits its higher costs of transport (Fig. 9).

In a general sense, though, as overall distances traveled during foraging increase, so too the costs of transport must decrease if such travel is to be profitable, which ultimately puts flying individuals at an advantage. The ability to travel large distances with minimum expenditure thus benefits birds accessing distant, known, stable, particularly productive areas for feeding (Fig. 9b, distance 2.5; Pinaud et al. [2005]), multiple, but widely spaced prey items (cf. Hein et al. [2004]), or patchy prey that might be only available for a short time (Weimerskirch et al. 2005*a*, *b*). None of these conditions is applicable for the Galápagos Cormorant.

Flightlessness and colony size and distribution

The availability of seabird resting sites (typically occurring at predator-free localities such as islands [Simeone et al. 2003]) interacts with speeds and costs of travel and intraspecific competition to modulate the profitability of foraging at different distances from the colonies (Furness and Birkhead 1984, Wanless and Harris 1993, Ainley et al. 2004). Where predator-free islands necessitate that colonies be widely spaced due to limited suitability of nesting sites, for example, birds with the most rapid, low-cost travel will have a competitive advantage to the detriment of other (particularly flightless) individuals. Where travel costs are particularly low, such islands may lead to high densities of seabirds (Velando and Freire 2001), which may benefit from a number of advantages of coloniality (Danchin and Wagner 1997). However, if, as in the Galápagos, the whole area is predator-free so that colonies may be located anywhere, and rapid drop-off in bottom topography precludes benthic-foraging species from hunting far from the coast, then flightless species may predominate, with large numbers of small colonies (Fig. 2b) being spaced along the coast (as is the case in the Galápagos Cormorant; Fig. 1).

This treatise concentrates on breeding birds, which are constrained to be central place foragers although it would seem that even non-breeding Galápagos Cormorants adhere to this. Mark–resight studies of banded breeders and nonbreeders (Harris 1979, Valle 1994) and this study (2003–2005), where more than 1200 cormorants were PIT- (passive integrated transponder) tagged and monitored at each colony, all show a strong philopatry. Birds tend to stay in the same colony. We agree with Snow's (1966) suggestion that the Galápagos Cormorant may be restricted by having to exploit highly productive feeding areas located near sheltered nesting sites. For example, although the western and southern coasts of Fernandina are productive areas, cormorants are absent due to the steep cliffs and rough seas which preclude these birds from landing (Fig. 1).

Flight and foraging underwater

The severe constraints on mass in flying birds (McNab 1994) have led to the universal use of air as an insulator rather than other options such as skin or fat, as are used in some mammals (cf. Weisel et al. 2005). This is problematic for birds that forage underwater, however, because the 700-fold difference in density between air and water means that air leads to upthrust in water whose extent, following Archimedes, is given by

$$\text{Upthrust} = 9.81(\text{Vol} \times \rho_w - \text{Vol} \times \rho_a) \approx 9.81\text{Vol} \times \rho_w \tag{2}$$

where Vol is the volume of air and ρ_w and ρ_a are the densities of water and air, respectively. The high density of water means that upthrust due to air in the plumage of birds is substantial (estimates range between about 1 and 5 N/kg body mass [Wilson et al. 1992, Stephenson 1993]) so that most of the energy used by diving birds underwater can be equated to working against it (Lovvorn and Jones 1991, Lovvorn 1999, 2001, Butler 2000). In order to minimize this, birds that routinely dive have reduced volumes of plumage air (Wilson et al. 1992), the most extreme case being cormorants, whose wettable plumage leads them to having only ~170 mL plumage air/kg mass (Gremillet et al. 2005*a*), compared to ~340 mL for diving ducks and auks (Wilson et al. 1992). This comes at a cost, however, since reduced air volumes mean reduced insulation and greater heat loss (Gremillet et al. 1998), something that explains why wettable plumage (Ribak et al. 2005*b*) is believed to have arisen in the tropics (Gremillet et al. 1999*b*, 2001, 2005*b*) and is only tenable in colder climes if ingestion rates are appropriate to pay for the high heat loss costs (Gremillet and Wilson 1999, Gremillet et al. 2004).

Air volume in the plumage is profoundly affected by depth, being reduced by increasing hydrostatic pressure according to Boyle's Law which, for seawater, can be expressed as

$$\text{Vol}_d = \text{Vol}_s/(1 + 0.097D) \tag{3}$$

where Vol_d is the volume of the air at any depth, Vol_s is the volume of the air at the surface, and D is the depth. Thus, upthrust from air in the plumage, which relates to the energy expenditure necessary to counteract it, varies with depth according to

$$\text{Upthrust} = 9.81\rho_w[\text{Vol}_s/(1 + 0.097D)]. \tag{4}$$

Thus, diving birds expend less energy counteracting upthrust due to plumage air with increasing depth.

The reduction in volume with increasing depth also affects heat loss though because the law of heat conduction gives the rate of heat flow as

$$dE/dt = \text{k}A(\Delta T/L) \tag{5}$$

where k is the constant of conductivity for the insulator in question (air), A is the transversal surface area, ΔT is the temperature difference, and L is the thickness of the insulator. Since k and A are constants in our general scenario and in an initial approach ΔT can be treated as a constant (but see *Discussion: Intersex differences in diving behavior*), the value of L critically determines the rate of heat loss and may be expressed in the following equation:

$$dE/dt = \text{k1}(\Delta T/L). \tag{6}$$

L will vary virtually linearly with plumage air volume so that

$$L = \text{k2} \times \text{Vol}_s \tag{7}$$

where k2 is a constant, so the expression can be rearranged using Eqs. 3 and 7 to give

$$dE/dt = \text{k1}\{\Delta T/[(\text{k2} \times \text{Vol}_s)/(1 + 0.097D)]\}. \tag{8}$$

If drag considerations are ignored (as being constant at constant speed), the overall plumage-air-related energy expended by a bird swimming underwater reflects a balance between decreasing mechanical power and increasing heat loss (Enstipp et al. 2005), with increasing depth (Quintana et al. 2007; Fig. 10a). An optimum balance between air volume and depth would mean that the heat generated by muscles working against buoyancy (Watanuki et al. 2003, 2005) would exactly balance that

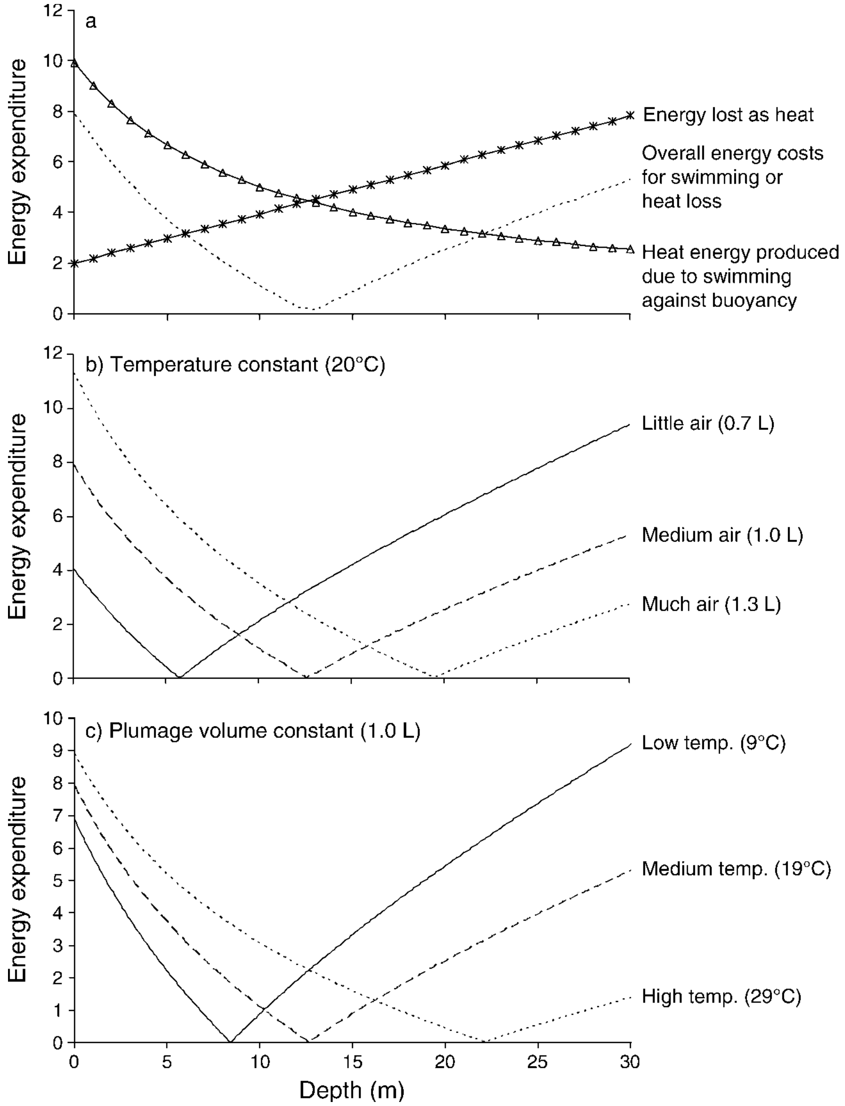

FIG. 10. (a) Energy expenditure: energy expended to counteract buoyancy decreases with depth, and heat loss increases with depth, both due to changing plumage air volumes. Note that this scenario ignores heat generated due to BMR and drag resulting from the speed (constant values for these will tend to shift the minimum energy expenditure point to the right). (b) Overall energy expenditure for a bird diving in water at constant temperature (cf. panel a) in relation to varying plumage air. As the air in the plumage increases, so too does the depth at which the minimum energy expenditure occurs. (c) Overall energy expenditure for a bird diving in water with a constant plumage volume at the surface (cf. panel a) in relation to varying water temperature. As the temperature increases, so too does the depth at which the minimum energy expenditure occurs.

lost through the reduced insulation. This would minimize metabolic rate and increase the relative time that birds could remain underwater. It should be noted, however, that this can only be achieved at one specific depth under conditions of constant temperature (Fig. 10b). Departures from this depth lead to birds operating suboptimally to a degree determined primarily by the volume of plumage air which affects the steepness of the energy vs. depth curve (Fig. 10c). Non-balance of mechanical vs. heat loss energy explains why Enstipp et al. (2006) noted an increase in expenditure in deep-diving over shallow-diving Double-crested Cormorants *Phalacrocorax auritus* and indicates just how critically choice of depth can affect the energetics of foraging in diving birds. It also shows how prey availability as a function of depth must vary to make foraging at a nonoptimal depth (in terms of energy expenditure) preferable.

Intersex differences in diving behavior

Valle (1994) points out that the Galápagos Cormorant is the most sexually dimorphic member of the Phalacrocoracidae. His explanations for this include disruptive selection due to niche differentiation between the sexes with, however, general directional selection for larger body size but with males increasing at a greater rate than females (Valle 1994). Below, we consider how differential size relates to features such as heat loss during foraging and how differences in foraging behavior might also drive selection for dimorphism.

The approach presented above assumes a constant water temperature. However, the data gathered from foraging birds show that temperature varies substantially with depth. Our knowledge of this can be incorporated into a model of heat loss as a function of depth based on Eq. 7 in tandem with Newton's law of cooling which, in our case, can be expressed as

$$dE/dt = \mathrm{c}(T_\mathrm{b} - T_\mathrm{e}) \tag{9}$$

where c is a constant derived from k, A in Eq. 5 and L in Eq. 6, and T_b and T_e are the temperatures of the bird and the environment, respectively, which relate to ΔT in Eq. 6 (cf. Dawson et al. 1999). Thus, the rate of heat loss as a function of environmental temperature and depth can be described by

$$dE/dt = \mathrm{k1}\{(T_\mathrm{b} - T_\mathrm{e})/[(\mathrm{k2} \times \mathrm{Vol_s})/(1 + 0.097D)]\}. \tag{10}$$

Using the general relationship between water temperature and depth derived from birds in all areas where they were equipped, Temp = 20.2 – 0.215(Depth) (see *Results: Temperature variation down the water column*), and assuming that Galápagos Cormorants have a body temperature of 39°C (cf. Wilson and Gremillet 1996, Gremillet et al. 1998; but see Schmidt et al. 2006 and references therein), it is possible to construct values for relative heat loss as a function of depth. Derived absolute values for heat loss would be subject to substantial assumptions but the invariance of even the multiple constants means that relative heat loss is likely to be a good approximation to reality, being based on well-established physical principles. This approach indicates that heat loss of cormorants in the Galápagos swimming at depths of 5, 10, 20, and 30 m would be about 1.5, 2.1, 3.4, and 5.0, respectively, times greater than that at 0.5 m. Eq. 10 allows elucidation of the extent to which male and female Galápagos Cormorants are exposed to differing relative heat losses according to the environments in which they choose to forage. This procedure (Fig. 11) shows a clear differentiation in the thermal environments used by the two sexes, with females exploiting the warmer waters more than the males. This difference is brought about by shallower dives (Fig. 6) and possibly active selection for warmer environments, something that is also reflected in the difference in the GPS-determined tracks.

We note that although some monomorphic seabirds, such as the Northern Gannet *Sula bassana*, may show intersex differences in foraging areas and the depth selected (Lewis et al. 2002), the consequences of being exposed to different thermal conditions has particular ramifications for Galápagos Cormorants because of the marked sexual dimorphism. Differences in size lead to differences in the volume : surface area ratio which tends to make larger animals less susceptible to the effects of cold (see Meiri and Dayan 2003). Using Walsberg and King's (1978) formulation for the relationship between bird body surface area and mass,

$$A = 0.0811m^{0.667} \tag{11}$$

where A is the surface area and m is the mass, the mean female Galápagos Cormorant, weighing 2.8 kg has a body surface area of 0.16 m^2 while that of the average male at 3.9 kg is 0.20 m^2. This translates into a difference in surface area : volume ratio of 11%, which should make the males correspondingly less prone to heat-loss problems.

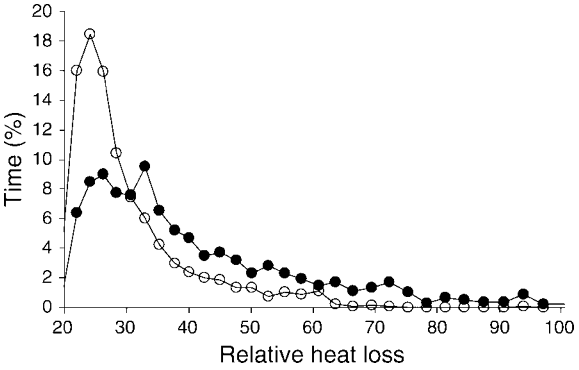

FIG. 11. Percentage underwater time exposed to differing heat-loss regimes according to temperature and depth for male (black circles) and female (open circles) Galápagos Cormorants.

The observation that each bird will have a depth at which energy expenditure is liable to be minimized (Fig. 10) allows us to put the situation of the Galápagos Cormorant into perspective intraspecifically and with respect to other members of the genus and world ocean temperatures. Other things being equal, at any given temperature, increasing air volumes in the plumage will tend to lead to a minimum energy expenditure (Fig. 10a) that occurs at correspondingly increasing depths (Fig. 10b). Conversely, for any particular species-specific volume of air in the plumage (cf. Gremillet et al. 2005 where plumage air volume in *Phalacrocorax carbo* was found to be invariant of locality), birds are expected to benefit most by diving deeper in warmer waters (Fig. 10c). Note also that the balance of temperature and depth, in modulating energy expenditure underwater, will theoretically affect how long any particular species can dive, something that might explain the curious intraspecific variability in dive duration vs. depth (cf. *P. capillatus* and *P. aristotelis* in Fig. 8). The Galápagos Cormorant has minute wings (Livezey 1992), a reduced density of short feathers (Cubo and Arthur 2000), and a large body mass, all features that will tend to reduce the mass-specific volume of plumage air and would tend to select for a bird that benefits most by foraging at shallower depths. This pattern would be reinforced by the temperature/depth profile around the Galápagos because, although the sea surface temperature is relatively high at ~20–22°C, water temperature drops rapidly with depth (Fig. 7b). However, where Galápagos Cormorants can operate in warm, shallow water, reduced upthrust and minimized heat loss might lead to particularly low energetic costs during diving. Evolution at a site where predators were absent may also help reduce energy and time spent in vigilance (Blumstein 2002, Blumstein and Daniel 2005, Blumstein 2006). Such reduced operational costs may allow them to survive under conditions of relatively low rates of prey acquisition, conditions typical of El Niño years, although clearly specific behavioral tactics, such as seeking cold pockets of water where fish may survive, could also play an important role in the species survival at such times.

Intra-sex differences in dive capacity, which have also been noted in other cormorant species (e.g., *Phalacrocorax albiventer* and *P. filamentosus*) with larger (by 15–20%) males diving deeper (Kato et al. 1999), can also be explained by consideration of plumage air volume. Our treatise assumes that both genders have equal mass-specific volumes of air. If, however, females have relatively less air, they would experience greater energy expenditure via heat loss than the males at depth, but would expend less mechanical energy at shallow depths than the males, while not being exposed to the reduced temperature conditions found at depth. Behavioral traits leading to differential area and habitat use (Table 2), particularly where such differences can be better exploited by one gender than another (Fig. 11), results in selection for niche separation that will tend to reduce intraspecific competition which is likely to be most severe in species with limited foraging ranges.

Conservation issues associated with flightlessness in the Galápagos Cormorant

Currently, only the upwelling areas around Fernandina and Isabela Islands provide reliable and sufficient food for the Galápagos Cormorant (Boersma 1978, Harris 1979, Tindle 1984), so it seems likely that there were no flightless cormorants before the emergence of Isabela and Fernandina above sea level some 0.5–1 million years ago. Additionally, there is no fossil evidence that the Galápagos Cormorant was more widespread in the past than it is now (Steadman 1986, Steadman et al. 1991). The time frame for the emergence of Isabela and Fernandina also agrees with the time of divergence of the Galápagos Penguin some 0.8 million years ago (Grant et al. 1994, Akst et al. 2002), this being another species dependent on upwelling to survive (Boersma 1978). In fact, the upwelling only occurs because the deeper Cromwell Current (also known as the Equatorial Undercurrent) flowing from west to east hits Fernandina and particularly Isabela Island, whose elongated and south–north orientation forces the water to the surface. Interestingly, recent research indicates many of the demersel fish on which the cormorants feed in western Galápagos are also endemic to the area (Edgar et al. 2004), so strong associations between fish and cormorants could have taken place under the particular conditions of the upwelling system that started as a result of the emergence of Isabela and Fernandina.

During El Niño, penguins die because the upwelling is suppressed or reduced (Valle and Coulter 1987) while, conversely, during La Niña, cormorants increase in density within Isabela and Fernandina without expanding their distribution to other islands; this occurs presumably because the upwelling is still concentrated around Fernandina and western–northern Isabela (Vargas 2006), although the water of other islands (e.g., Floreana) gets colder due to the influence of the "cold tongue," which is fed by cool waters of the South Equatorial Current (Koutavas et al. 2002).

We argue that the Galápagos Cormorant is highly specialized to exploit its own particular environment, this consisting of the few areas of the Galápagos Archipelago where upwelling leads to locally enhanced productivity in shallow, tropical waters. Since high degrees of specialization make species more susceptible to extinction (Henle et al. 2004, Julliard et al. 2004), a condition that is particularly problematic in the tropics (Stratford and Robinson 2005), and the world population for the Galápagos Cormorant is currently estimated at less than 1000 pairs (Valle and Coulter 1987, Valle 1995, Vargas et al. 2005) and restricted to the west coast of only two islands, the species is classified as endangered on the IUCN Red List (BirdLife International 2000, Adams et al. 2003). Flightlessness precludes this bird from being able to exploit patchy, widely spaced prey or distant prey, and the supposed reduced air in the plumage means that it is probably ill-adapted to exploiting prey either in cold water or at depth. Although El Niño tends to raise water temperatures by up to 4°C above the long-term mean (Glynn 1988, Vargas et al. 2006), which would reduce relative heat loss by a factor of over 10%, the energetic gains in this are likely to be more than offset by the detrimental changes in prey distribution and abundance brought about by El Niño (Chavez et al. 2002, Franco-Gordo et al. 2004). This explains why Galápagos Cormorants did not breed during the 1982–1983 El Niño (Valle et al. 1987). At such times, the large mass of this species may also help reduce the risk of starvation (cf. Blanckenhorn 2000). Nonetheless, the Galápagos Cormorant is also characterized by its apparent success during La Niña years because population crashes during El Niño events are generally followed by rapid recovery (Valle 1995; cf. Ainley et al. 1995). Given that the particular conditions necessary for Galápagos Cormorant breeding success only occur in a very small part of the Galápagos Archipelago (Rosenberg et al. 1990), we suggest that populations of this species were never very high and are unlikely to reach high levels in the future. Two major elements combine to endanger the Galápagos

Cormorant: First, it has been suggested that the incidence of El Niño events may be increasing (Karl and Trenberth 2003). Second, the direct effects of man are substantial. These include fishing practices, which may alter the seabed, deplete benthic fish populations, and cause birds to drown in nets (Valle 1995, Vargas et al. 2006), oil spills (Edgar et al. 2003), and introduction of predators (cf. Boersma 1998) and disease (Gottdenker et al. 2005; Travis et al., *in press*). Ultimately, judicious management by man and the extent of the remarkable capacity of this species to flourish in good years will determine whether the population can remain viable in the foreseeable future.

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