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Oxygen stores and foraging behavior of two sympatric, planktivorous alcids

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ABSTRACT: Seabird species with overlapping diets commonly coexist at breeding colonies. For example, ancient murrelets *Synthliboramphus antiquus* and Cassin's auklets *Ptychoramphus aleuticus* are similar-sized small alcids that feed on krill and small fish. Little is known regarding their partitioning of aquatic resources, so we assessed the O_2 stores and foraging behavior of sympatrically breeding populations of these species. The attachment of recorders (1 to 3% of body mass) caused substantial nest desertion, but we reduced these effects by only equipping experienced birds early in the day. Auklets and murrelets had 18 to 24% higher mass-specific O_2 stores than slightly larger non-diving kittiwakes *Rissa tridactyla*. When compared to published values, blood hemoglobin content was higher, muscle pH buffering capacity was similar and muscle myoglobin content was lower for small divers than for larger non-phocid divers. The slightly higher O_2 stores of Cassin's auklets was reflected in their aquatic behavior, as auklets dived longer than murrelets at any given dive depth. Moreover, chick-rearing auklets spent 31% more time underwater than incubating auklets and 50% more time underwater than incubating murrelets. In total, 45% of dives by chick-rearing auklets, 36% of dives by incubating auklets and 13% of dives by incubating murrelets exceeded their estimated aerobic dive limits. Murrelets primarily used V-shaped dives while auklets generally exhibited W-shaped dive profiles with a protracted bottom phase. Thus the O_2 stores and foraging behavior of the 2 sympatric seabirds differed.

KEY WORDS: Cassin's auklet · *Ptychoramphus aleuticus* · Ancient murrelet · *Synthliboramphus antiquus* · Reef Island · Haida Gwaii · Hemoglobin · Myoglobin

INTRODUCTION

Maximum dive duration scales strongly with body mass, so that for fixed transit times small animals are limited to brief access to their prey and hence are under strong selection to increase time available for foraging underwater (Watanuki & Burger 1999, Halsey et al. 2006). Small size also restricts the size of devices that can be used to monitor underwater behavior, and most of what is known about the at-sea behavior of small divers has been obtained from observations at the surface (Hunt et al. 1998). However, recent advances in the miniaturization of electronic recorders now permit detailed examinations of the free-ranging dive profiles of some of the smallest marine endotherms, the planktivorous alcids (Harding et al. 2009).

The planktivorous alcids (Alcidae) form an important component of North Pacific marine ecosystems, yet the behaviors by which they detect and procure prey underwater remain virtually unknown (Burger & Powell 1990). Thus, although parameters measurable at the colony, such as reproductive success and survival, suggest a strong effect of ocean climate on the biology of North Pacific planktivorous alcids (Abraham & Sydeman 2006, Hipfner 2008, Wolf et al. 2009), the physiological mechanisms that mediate between free-ranging populations and their prey remain speculative. Our ability to understand the plasticity of planktivorous birds to oceanographic change and to interpret changes in demographic measures depends on a thor-

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ough understanding of the mechanisms that link zooplankton abundance to demography through foraging behavior. Unfortunately, little is known regarding the factors underlying the breath-hold capabilities or at-sea behavior of these diminutive divers.

In terrestrial ecosystems, apparently similar sympatric species often actually occupy somewhat different niches (e.g. Grant & Grant 2002). In marine ecosystems, some sympatric large-bodied animals (penguins and seals) possess differences in O_2 stores and segregate based on dive depth, with one species feeding on high density prey at depth and another on low density prey nearer the surface (Trivelpiece et al. 1987, Mori & Boyd 2004). Other sympatric large-bodied species show similar dive abilities but segregate based on foraging locations (Trivelpiece et al. 1987, Hull 1999) or timing of foraging activities (Bailleul et al. 2005, Luque et al. 2007). In contrast, the mechanisms underlying the partitioning of aquatic resources among sympatric populations of small seabirds remain unclear. Twenty species of alcids inhabit the North Pacific and surrounding waters, including 9 species that are primarily planktivorous and several more that are partially planktivorous. As planktivorous alcids are often sympatrically distributed and exploit similar prey items (Hunt et al. 1998), they present excellent model systems for examining how marine animals partition their niches.

Cassin's auklets *Ptychoramphus aleuticus* and ancient murrelets *Synthliboramphus antiquus* breed sympatrically in the Haida Gwaii archipelago off the Pacific coast of British Columbia. Stomach contents obtained from both species collected at-sea contained larval fish and *Thysanoessa* euphausiids; auklet stomachs also contained copepods, while murrelet stomachs also contained *Euphausia pacifica* (Sealy 1975, Vermeer et al. 1985). The 2 species represent examples of the 2 main planktivorous alcid clades: the auklets (single egg, long chick-rearing period at the colony, feet placed more anterior) and murrelets (2 eggs, chicks are precocial and leave the colony at 2 days of age, feet placed more posterior). To better understand the behavioral underpinnings of resource competition between these species, we initiated a study using time-depth-temperature recorders (TDTRs) to examine their flight durations and at-sea dive profiles. To identify physiological mechanisms accounting for underwater endurance and at-sea dive profiles, we also measured muscle myoglobin and buffering capacity, assayed blood hemoglobin and hematocrit and estimated total body O_2 stores of both species. As these birds have body masses at the lower limit of those considered acceptable for available instruments, we also investigated the impact of the devices on desertion rates to provide guidelines for future research. The Gwaii Haanas National Marine Conservation Area, adjacent to Reef Island, is currently in the planning phase. Thus knowledge of what depths and foraging radii auklets and murrelets utilize could be useful for selecting areas to protect that maximize benefit to these birds.

MATERIALS AND METHODS

Effect of instrumentation. All deployments occurred at Reef Island, Haida Gwaii (52.93° N, 131.54° W). Birds were captured during the daytime either in nestboxes (most ancient murrelets) or in natural burrows (all Cassin's auklets and 2 murrelets) and instrumented with TDTRs. The only exceptions were chick-rearing auklets, 3 of which were captured using mist nets during nighttime, and 8 incubating ancient murrelets also obtained during nighttime using nets that knocked them to the ground (knock-down nets), at which time they were immediately captured by hand. Upon recapture, TDTRs were removed, birds were weighed to the nearest gram and a small blood sample was taken on protein-saver paper for sexing using PCR. Handling time was <3 min for both capture and recapture protocols.

We attached devices 27 April to 20 May 2008 and 28 April to 12 May 2009. We attached cylindrical Lotek 1100LTD TDTRs (sampling interval = 3 s, memory = 128 kB, mass = 5 g, diameter = 1 cm, length = 3.3 cm, accuracy ± 2 m; Elliott & Gaston 2009) to 10 incubating murrelets and 6 auklets in 2008 and 5 murrelets and 5 incubating and 3 chick-rearing auklets in 2009. The devices were attached with duct tape to a metal band, which was then attached to the foot with the pressure sensor facing posterior. In 2009, we also attached 1500LAT TDTRs (sampling interval = 1 s for auklets and either 4 or 12 s—with 1 s sampling when depth was >2 m—for murrelets; memory = 512 kB, mass = 2.8 g, diameter = 0.5 cm, length = 3.3 cm, resolution ± 0.25 m) to 8 incubating murrelets, 2 incubating auklets and 1 chick-rearing auklet. In addition, we deployed 18 maximum depth gauges (MDGs; 80 mm Tygon tubing powdered with icing sugar so that maximum pressure could be deduced from where the icing sugar was washed away by sea water following Elliott & Gaston 2009) on 18 murrelets (10 in natural burrows in the daytime and 8 in knock-down nets at night) and 5 auklets (all in natural burrows) in 2008.

In 2008, to compare various potential treatments, we also attached dummy (candle wax and lead shot) devices of different sizes (2.8 and 5 g) and design (back-mounted, N = 6; leg-mounted, N = 5; leg-mounted attached by cable tie without removing the bird from the burrow, N = 5) to ancient murrelets (5 for each treatment) in natural burrows.

Physiological parameters and O_2 stores. In 2008, blood samples were taken from 10 non-breeding (lacking a brood patch) ancient murrelets captured at night and 10 incubating auklets (5 captured during the day, 5 at night). Samples were obtained from the brachial vein using a 27 gauge needle and 1 ml syringe, and transferred into heparinized microhematocrit tubes. Hematocrits were measured in duplicate following a 5 min spin. The remaining capillary tubes were emptied into cryovials and immediately frozen in liquid nitrogen until return to the laboratory, where hemoglobin concentration was measured using the cyanmethemoglobin method (Sigma diagnostics total hemoglobin procedure no. 525, which states that blood frozen up to 1 yr is suitable for analyses; a 20 µl blood sample from each individual was also placed in 5 ml of Drabkin's solution at the time of collection and frozen; both procedures gave similar results). Standards were prepared from lyophilized human hemoglobin (Sigma Hemoglobin Standard no. 525-18). Samples were diluted to obtain values within the standard curve, and the hemoglobin concentrations calculated by dividing the measured value by the percent dilution. We did not filter or centrifuge the samples as no turbidity was observed, probably because the birds were captured at the colony and had not eaten recently. Hematocrit samples were also obtained from 10 non-breeding and 10 breeding ancient murrelets in 2009.

In 2008, we also euthanized 5 non-breeding murrelets and 5 breeding auklets by cervical dislocation following blood collection. The heart, right leg muscle (sartorius and gastrocnemius) and a portion of the right breast muscle (pectoralis and supracoracoideus) were immediately dissected free, weighed to the nearest 0.1 g and placed in a −70°C nitrogen shipper together with the remaining carcass. Non-muscle portions of the bird (e.g. alimentary tract, skin, brain) were removed and the carcass was re-weighed and placed in a heated solution containing the enzyme papain, Bio-Ad detergent and EDTA for 48 h (MacArthur et al. 2001). The mass difference following this treatment was ascribed to muscle and hence added to the breast, leg and heart muscle weights to obtain a total estimate of body muscle mass. For comparative purposes, blood and muscle samples were also obtained from 5 black-legged kittiwakes *Rissa tridactyla* and 5 thick-billed murres *Uria lomvia* collected at Prince Leopold Island in 2008. Heart, leg and breast muscle subsamples from each of the 4 avian species were analyzed for myoglobin concentration using the methods of Reynafarje (1963). Briefly, we homogenized ~0.5 g of muscle in a low ionic strength phosphate buffer (19.25 ml buffer per 1 g of wet tissue) using a mechanical tissue grinder submerged in an ice bath (MacArthur et al. 2001). The homogenate was then centrifuged at 11 000 × *g* for 1.5 h at 5°C, and 4 ml of supernatant was transferred to a custom-built glass vial through which carbon monoxide was bubbled for 8 min. Excess sodium dithionite was added and carbon monoxide bubbled for an additional 2 min to assure complete reduction. The supernatant was then placed in a cuvette and absorption was read at 538 and 568 nm and converted to myoglobin concentration following Reynafarje (1963).

Total O_2 stores (T_{O_2}) for each individual was estimated as:

$$T_{O_2} = 0.9 \times 0.176 \times 0.1608M^{0.91} + 1.34M_bM_m + B_{O_2}$$

where the first term is the respiratory O_2 stores of a bird of mass M (kg), assuming respiratory volume followed the allometric relationship determined by Lasiewki & Calder (1971), that 17.6% of lung volume was O_2 and 90% of lung O_2 stores were usable (Croll et al. 1992, Knower Stockard et al. 2005). The second term is the muscle O_2 stores, where M_m is body muscle mass (g), assuming that each gram of myoglobin can bind 1.34 ml O_2 (Ponganis et al. 1997). We assumed that all muscle that was not heart or breast had a myoglobin concentration (M_b) similar to the leg. The third term, blood O_2 stores B_{O_2}, was estimated as:

$$B_{O_2} = 0.96 \times 1.34\,(0.95 \times 0.3 + 0.7 \times 0.7)H \times 0.123M$$

Blood hemoglobin content (H, g dl^{-1}) was measured directly. We assumed blood volume was 12.3% of body mass in g (as determined for murres; Croll et al. 1992), the O_2 binding capacity of hemoglobin was 1.34 ml g^{-1} pigment (Tamburrini et al. 1994), 30% of the blood was arterial at 95% O_2 saturation and 70% was venous at 70% saturation, and 96% of O_2 was usable (Croll et al. 1992).

The buffering capacity of pectoralis muscle, defined as the amount of base required to raise the pH of 1 g of wet muscle from 6 to 7, was determined following the procedure of Castellini & Somero (1981). This entailed homogenizing ~0.5 g muscle subsamples in 0.9 M NaCl, followed by titration at 37°C with a 0.2 M NaOH solution using an Accumet AB 15/15+ pH meter equipped with an AccuTupH sensing electrode (Fisher Scientific).

We also compiled data for hematocrit, hemoglobin content, myoglobin concentration and buffering capacity in birds and mammals from the literature and correlated these values with body mass. Separate correlations were conducted for terrestrial and aquatic and/or semi-aquatic animals. Terrestrial, aquatic (freshwater diving) and marine (marine diving) animals were analyzed separately to assess whether any of the above traits differed among these 3 groups. All correlations were completed on log-transformed values. Unless otherwise noted, all values are presented as means ± 1 SE.

Foraging behavior. Due to device uncertainty, only depths >2 m were considered dives. A custom-designed Visual Basic macro corrected for passive electronic drift (based on the last 10 consecutive, identical pressure values before the dive), converted the pressure linearly into depth (1.00 m = 1.00 dbar = 1.41 psi) and was used to calculate ascent and descent rates, maximum depth, dive duration and surface pause duration.

We defined surface pauses as anticipatory if they correlated better with the following dive duration and reactive if they correlated better with the previous dive duration, with the former representing bout structure where birds anticipate subsequent dive durations and required O_2 stores and the latter representing bout structure where birds react to previous dive durations and lactate build-up (Jodice & Collopy 1999, Elliott et al. 2007, 2008b). We divided dives into bouts using the sequential differences method and a 2-process exponential model, where one process is the random distribution of events, or dives, within a bout, and the other process is the random distribution of events, or bouts (criterion: 70 s surface interval differences for murrelets, 90 s for auklets; Mori et al. 2001). A 1-process exponential model would mean that dives were randomly distributed across time and not organized into bouts. The temperature log was used to classify the time devoted to the following activities: (1) flying (temperature variable and medium); (2) resting on the surface (temperature constant and low, or constant and very high when the bird tucked its foot into its plumage); and (3) at the colony (high temperature, low pressure). We also obtained regurgitations from 4 chick-rearing auklets captured at night.

We estimated maximum possible foraging radii, assuming an estimated flight speed of 55 km h^{-1} (Elliott et al. 2004). When flying is broken into bouts the maximum distance traveled from the colony is generally less than estimated assuming all flights are directed away from or towards the colony. In that case, the actual feeding area is probably much closer to the colony than the maximum distance estimated from total flight time (Thaxter et al. 2009, Elliott et al. 2009a), so our values are likely overestimates.

RESULTS

Effect of instrumentation

In 2008, 7 of 10 ancient murrelets and 5 of 6 incubating Cassin's auklets equipped with the 5 g TDTRs deserted (Table 1). Murrelets equipped with MDGs in natural burrows during the daytime (11 of 15) or using knockdown nets in the nighttime (8 of 9) showed a high rate of abandonment, though it is possible that birds initially caught in knockdown nets may have avoided the nets during subsequent nights rather than deserting. Auklets equipped with MDGs also had low return rates (2 of 3 incubating birds and 0 of 1 chick-rearing bird). Excluding MDGs, we recaptured 9 of 26 murrelets (35%) and 1 of 6 incubating auklets (17%) in 2008. In contrast, seabirds equipped with 2.8 or 5 g TDTRs in 2009 had much higher recapture rates (12 of 13 or 92% of murrelets, 7 of 8 or 88% of incubating auklets, and 4 of 4 or 100% of chick-rearing auklets). Overall recapture rate, excluding MDGs, in 2009 (23 of 25) was higher than that in 2008 (10 of 32; Fisher's exact test, $p < 0.00001$).

Physiological parameters, O_2 stores and aerobic dive limits

Auklets had higher hematocrit ($t_{19} = 2.45$, $p = 0.02$), myoglobin concentration ($t_9 = 2.53$, $p = 0.03$) and muscle buffering capacity ($t_9 = 3.85$, $p = 0.004$) than murrelets, but similar hemoglobin concentration ($t_9 = 1.83$, $p = 0.09$). In total, auklets possessed 5% higher mass-specific O_2 stores than murrelets, suggesting somewhat greater specialization for longer dive durations. Auklets had 24% and murrelets 18% higher O_2 stores per gram of body mass than the slightly larger non-diving kittiwake (Table 2). The slightly higher O_2 stores (relative to body mass) in auklets are unlikely to be due to the murrelets being non-breeders and the auklets being breeders, as hematocrit values were similar in non-breeding and breeding murrelets (Table 2). This is despite the fact that breeders spent 1 to 3 d in the burrow prior to sampling, presumably resulting in some dehydration.

Foraging behavior

We obtained free-ranging flight and dive data on 12 incubating ancient murrelets (2 additional birds returned, but logs were corrupted or data otherwise lost and we obtained data from one bird in both years) and 8 incubating and 4 chick-rearing Cassin's auklets (Table 3). We also retrieved 4 of 10 MDGs deployed on murrelets at natural burrows and 1 of 8 MDGs deployed using knockdown nets, and 2 of 4 MDGs deployed on auklets.

Auklets dove for longer than murrelets, while murrelets dove slightly deeper, meaning that auklets remain submerged for 60% longer than murrelets at any given dive depth (depth: Kruskal-Wallis $\chi^2 = 243.2$, df = 2, $p < 0.00001$; duration: $\chi^2 = 1126.2$, df = 2, $p < 0.00001$) (Fig. 1, Table 2). There was no difference in dive depth

Table 1. Device effects on alcid mass loss, provisioning rates and recapture rates. F: females only; M: males only. Device mass was measured as % body mass; S: device was sutured; I: device was surgically implanted. Also shown are adult body mass loss during deployment (or relative to control post-deployment); provisioning rate (feeds or trips for murres and razorbills; chick growth rate for auklets and puffins) relative to control (parentheses: chick relative fledging success); and recapture or non-abandonment rates of equipped birds excluding birds losing devices (where available, apparent annual survival is shown in parentheses followed by annual survival for control birds; battery cycle is shown for one study that suggested this was an important parameter, Hatch et al. 2000)

Species	Device mass	Body mass loss (%)	Provisioning rate (%)	Recapture rate (%)	Source
Probable non-breeding					
Xantus' murrelet	1.8 S			(4.5; 6.6)	Newman et al. (1999)
Incubating					
Ancient murrelet	2.5			50 (leg, N = 20)	
				33 (back, N = 6)	
				40 (leg, in burrow[a], N = 5)	Present study
	1.3			88 (N = 9)	Present study
	1			88 (23; 77, N = 17)	Present study
Cassin's auklet	2.5			42 (N = 12)	Present study
	1.3			100 (N = 2)	Present study
	1.7			42	Ackerman et al. (2004)
Common murre	0.7			0	Wanless et al. (1985)
Marbled murrelet	5 I,S			(harness/suture/ surgery: 0; glue: 78)	Quinlan & Hughes (1992)
Incubation/chick-rearing unspecified					
Common murre	3.9 I		(–100)	(50; short cycle battery)	Meyers et al. (1998),
				(53–73; long cycle battery)	Hatch et al. (2000)
Dovekie	3.3	–1.8		63	Harding et al. (2009)
Thick-billed murre	3.9 I		(–100)	(0; short cycle battery)	Meyers et al. (1998),
				(57; long cycle battery)	Hatch et al. (2000)
Tufted puffin	4.9 I			(0; short cycle battery)	Meyers et al. (1998),
				(50; long cycle battery)	Hatch et al. (2000)
Chick-rearing					
Cassin's auklet	1.3–2.5			100 (N = 4)	Present study
	1.7		–44 (–33)	100	Ackerman et al. (2004)
	1.3			100	N. Karnovsky pers. comm.
Common murre	0.7		–61	87 (98)	Hamel et al. (2004)
	0.7		–30	100	Wanless et al. (1988)
	0.7			100	Wanless et al. (1985)
	0.5			60	Hedd et al. (2009)
	2.7	–3.2	–33	100	Tremblay et al. (2003)
Razorbill	1.2		–1	100	Wanless et al. (1988)
	3.2	–2.6		93	Dall'Antonia et al. (2001)
Thick-billed murre	0.5	–1.0	+16	100 (91; 92)	Elliott et al. (2008a)
	1.5	–5–10	–64	100	Watanuki et al. (2001)
	1.7	–0.7	(–22)	67	Takahashi et al. (2008)
	2.9	–3.7	–43	100	Elliott et al. (2008a)
(F)	2.7	–2.9	–64 (0)	100 (85; 96)	Paredes et al. (2005)
(M)	2.4	–2.8	–67 (0)	100 (80; 96)	Paredes et al. (2005)
	3.0	–1.0		100	Falk et al. (2002)
	3.3	–1.6		100	Croll et al. (1992)
Tufted puffin	1.2		(–61)	92	Whidden et al. (2007)

[a]Devices were attached using a cable tie with a single hand to birds in natural burrows without removing the bird from the egg chamber

and duration between incubating and chick-rearing auklets (Mann-Whitney U = 1298633, n_1 = 1447, n_2 = 2007, p = 0.51), but chick-rearing auklets dove more often (362 ± 10 dives d^{-1}, Table 3) than incubating auklets (276 ± 31 dives d^{-1}; t_{10} = 2.48, p = 0.03), as did incubating murrelets (387 ± 51 dives d^{-1}; t_{10} = 2.42, p = 0.04). Thus chick-rearing auklets spent 31% more time underwater than incubating auklets and 50% more time underwater than incubating murrelets (incubating auklets thus spent 15% more time underwater than incubating murrelets). Surface pauses tended to be anticipatory rather than reactive (ΔAkaike's information criterion [AIC] = 104.3), and tended to correlate better with subsequent dive duration than with depth (ΔAIC = 493.9). Incubating auklets had 5.4 s shorter surface pauses than incubating murrelets for a given dive dura-

tion (residual surface pause on dive duration, t_{8182} = 44.6, p < 0.00001), while chick-rearing auklets had 5.4 s shorter surface pauses than incubating auklets for a given dive duration (t_{2429} = 28.7, p < 0.00001) (Fig. 1).

The maximum foraging radius, given the total time spent flying, was 66 km (198 km for 3 d trips) for murrelets and 53 km for auklets (Table 4).

Murrelets showed higher transit rates than auklets (paired t_{19} = 7.15, p < 0.0001 when paired across bins) (Fig. 2), and exhibited V-shaped dives rather than the W-shaped dives favored by auklets (Fig. 3). Thus auklets presumably searched for prey through the water column (low transit rates, higher within-bout variation in dive depth) and likely consumed multiple prey items at different depths (wiggle dives). This contrasts sharply with the murrelet strategy, which entailed rapid dives to a defined depth (~9 m). Both species showed a 1-process model for sequential differences in depth, suggesting no bout structure in dive depth, but a 2-process model for surface pause intervals, suggesting that surface intervals provided bout structure (Fig. 1). Neither species dove at night, with diving starting 1 h before sunrise and ending 1 h after sunset (Fig. 4). Auklets provisioning with fish tended to have slightly deeper (mean = 3.1 m; Table 2), V-shaped dives, while those provisioning with krill tended to have wiggle dives (Fig. 1). Dive depth (but not frequency) increased with tide height for murrelets (depth: t_{199} = 4.176, p < 0.0001; frequency: t_{199} = 0.37, p = 0.71; frequency: t_{199} = 1.99, p = 0.05).

Diet

Two auklets regurgitated red krill *Thysanoessa spinifera* and 2 auklets regurgitated fish matter.

DISCUSSION

Effect of instrumentation

The 2009 recapture rates were comparable to those obtained from murrelets equipped with 1 g radio transmitters (with similar rates for birds with and without antennae; Table 1). Differences between the 2 years included: placement of TDTRs in the evening to maximize recording time in 2008 versus in the morning in 2009; and checking the box each day for murrelets after Day 2 of attachment in 2008 versus waiting 5 d before checking nest boxes to see if the banded bird was present or, alternatively, attaching a 1 g radio transmitter to the other leg so we could tell remotely if the bird was present.

The main factor affecting probability of abandonment in murrelets was whether the bird had been previously banded. In 2009, all except 4 recaptured TDTR-equipped birds (1 of which abandoned) were banded in 1984–2007, as were all but 1 (which abandoned) of the radio-equipped birds. Previously banded birds may be less likely to abandon because: (1) they tend to be older and less likely to sacrifice current reproduction for future survival; (2) they have been

Table 2. Oxygen storage parameters for 4 charadriiform birds (N = 5 for muscle parameters; N = 10 for blood parameters). Murrelets were non-breeders, and the remaining birds were breeders. Values are given as means ± 1 SE

Parameter	Cassin's auklet (small diver)	Ancient murrelet (small diver)	Thick-billed murre (large diver)	Black-legged kittiwake (small non-diver)
Mass (g)	171 ± 2	197 ± 7	980	359 ± 6
Usable respiratory O_2 stores (ml kg^{-1})	30.1	29.3	25.1	28.4
Hematocrit	53 ± 1	51 ± 1[a]	48 ± 1[a]	44 ± 2
Hemoglobin content (g dl^{-1})	20.7 ± 0.6	19.6 ± 0.9	18.1 ± 1.0	15.8 ± 1.0
Blood volume (ml)	21 ± 2	24 ± 2	121 ± 9	44 ± 4
Usable blood O_2 stores (ml kg^{-1})	26.9 ± 1.8	25.9 ± 2.0	23.5 ± 2.0	20.9 ± 1.9
Myoglobin concentration – breast (g kg^{-1})	10.6 ± 0.3	10.0 ± 0.2	13.5 ± 2.4[b]	4.2 ± 0.5
Myoglobin concentration – leg (g kg^{-1})	8.0 ± 0.4	9.4 ± 0.5		
Myoglobin concentration – heart (g kg^{-1})	6.3 ± 0.3	6.1 ± 0.9	6.3 ± 0.5	5.9 ± 0.7
Right *Pectoralis* mass (g)	11.2 ± 0.3	12.5 ± 0.3	71 ± 4	24 ± 1
Right *Supracoracoideus* mass (g)	3.4 ± 0.7	3.4 ± 0.2	23 ± 2	2.5 ± 0.6
Right leg and pelvic muscle mass (g)	3.9 ± 0.2	4.0 ± 0.2		
Heart mass (g)	1.8 ± 0.1	1.9 ± 0.1	9.4 ± 0.6	4.7 ± 0.1
Total wet muscle mass (g)	47 ± 1	52 ± 1	298 ± 10	80 ± 2
Muscle O_2 stores (ml kg^{-1})	3.6 ± 0.4	3.4 ± 0.4	2.8 ± 0.4	1.3 ± 0.1
Total usable O_2 stores (ml kg^{-1})	61 ± 2	60 ± 3	51 ± 2	50 ± 2
Total usable O_2 stores (ml)	10.4 ± 0.4	11.8 ± 0.5	50.0 ± 2.2	18.0 ± 0.8
Buffering capacity (slyke)	72 ± 2	64 ± 2	75 ± 3	52 ± 4

[a]Value for incubating murrelets = 53 ± 3, which was not significantly different from non-breeding murrelets (t_{27} = 1.85; p = 0.07); value for incubating murres presented
[b]Reported as 19 ± 2 by Croll et al. (1992)

Table 3. *Synthliboramphus antiquus* and *Ptychoramphus aleuticus*. Dive parameters (±SD) for ancient murrelets and Cassin's auklets equipped with 5 g (5) and 2.8 g (3) temperature-depth-time recorders (TDTRs). The last 4 birds were chick-rearing and regurgitated either euphausiids (E) or fish (F). F: female; M: male. Individual dive depths and durations for murrelets and auklets are available in Tables S1 and S2, respectively

Species	Sex	Bird ID	TDTR	Year	Mass (g)	No. dives (d^{-1})	Max depth (m)	Average depth (m)	Max duration (s)	Average duration (s)
Ancient murrelet	F	01047	5	2008	206	256	32.1	14.7 ± 7.8	69.5	39.6 ± 16.9
	F	01047	3	2009	nd	654	20.5	6.2 ± 3.3	55.9	16.3 ± 10.6
	M	DN2	5	2008	200	758	36.8	11.0 ± 5.2	69.5	29.8 ± 11.2
		90460	5	2008	199	367	19.4	8.3 ± 4.1	50.1	22.5 ± 9.7
	M	01002	5	2009	nd	263	26.7	12.0 ± 7.3	68.1	34.8 ± 18.3
	F	56514	5	2009	nd	208	23.3	13.6 ± 5.6	64.7	39.6 ± 12.6
	M	90531	5	2009	195	395	24.9	8.2 ± 5.5	64.3	23.3 ± 13.6
	M	01067	3	2009	209	207	21.0	9.1 ± 3.8	65.7	26.8 ± 12.2
	F	90460	3	2009	209	460	25.8	9.2 ± 4.2	65.4	18.3 ± 13.1
		90527	3	2009	198	427	25.3	6.7 ± 4.1	64.7	19.3 ± 13.6
	F	53431	3	2009	215	285	15.0	5.8 ± 2.0	45.6	14.3 ± 6.6
	M	53433	3	2009	202	414	25.8	9.7 ± 5.4	63.5	25.0 ± 14.1
		01004	5	2009	198	436	20.6	7.3 ± 3.5	62.9	22.5 ± 10.2
Mean					203 ± 6	387 ± 177	24.4 ± 5.6	9.4 ± 2.8	62.3 ± 7.3	25.5 ± 8.3
Cassin's auklet		UB2008	5	2008	182	213	24.8	13.7 ± 4.8	101.3	60.7 ± 18.6
	M	03901	5	2009	nd	194	12.8	5.6 ± 2.4	72.0	25.2 ± 16.6
	F	03902	3	2009	nd	304	23.5	7.4 ± 4.5	102.7	30.5 ± 24.7
	F	03903	3	2009	nd	413	20.0	5.9 ± 3.2	83.2	17.4 ± 15.7
	F	03904	5	2009	nd	328	22.8	5.9 ± 3.8	90.2	20.6 ± 16.2
	M	03905	5	2009	nd	248	24.7	11.8 ± 5.4	84.6	45.2 ± 20.6
	M	03906	5	2009	nd	156	25.4	14.3 ± 5.1	87.0	58.0 ± 17.8
	M	UB2009	5	2009	181	351	23.4	7.2 ± 3.7	83.0	31.3 ± 16.7
(E)	F	03908	5	2009	182	347	23.3	7.8 ± 4.0	87.7	35.6 ± 18.5
(F)	M	03912	5	2009	204	343	28.1	9.8 ± 5.9	97.5	40.9 ± 21.2
(E)	M	03914	5	2009	185	375	17.3	6.3 ± 2.9	71.4	26.7 ± 18.1
(F)	F	03918	3	2009	170	382	22.6	10.5 ± 5.1	88.5	39.9 ± 20.5
Mean					184 ± 11	305 ± 82	22.4 ± 4.0	8.9 ± 3.1	87.4 ± 9.9	36.0 ± 13.7

handled previously with no negative consequence and therefore are accustomed to handling; or (3) birds that are sensitive to handling do not return to the nest boxes. Similarly, 13% of non-previously banded thick-billed murres abandoned while 0% of previously banded birds deserted following attachment of monitoring devices (K. H. Elliott unpubl. data). As the corticosterone stress response decreases with age in seabirds, perhaps young, unbanded birds abandon because they have a stronger stress response to handling (Newman et al. 2005, K. H. Elliott unpubl. data).

Although our sample sizes for dummy treatment groups were small due to ethical considerations (n = 5 to 6 per group), we suggest the following guidelines for attaching recording equipment to small alcids based on data provided in Table 1: (1) use previously banded birds or choose well-established parts of the colony to avoid encountering inexperienced birds; (2) attach devices to the leg (minimizes body drag, but alters balance) or back, as both methods cause statistically insignificant differences in desertion (back: 33% recapture rate for murrelets; leg: 48%), but avoid use of surgery (surgery: 28% recapture rate averaged across Table 1; no surgery: 83%); (3) attach the devices early in the day, as done in 2009, as this may allow stress to return to baseline before nightfall; (4) minimize disturbance to the bird and its partner, as done in 2009 (the partner may be able to compensate for disrupted behavior in the equipped bird, Paredes et al. 2005); (5) remove the bird from its burrow for easier handling (removal: 48% recapture rate for murrelets; non-removal: 40%); and (6) use chick-rearing birds, as they are less likely to abandon (incubation: 40% recapture rate averaged across Table 1; chick-rearing 95%). Although at other locations females are less likely to abandon than males (Ackerman et al. 2004, Paredes et al. 2005), there was no sex bias in the birds we equipped successfully (we only sexed our birds upon return), suggesting that we had a similar desertion rate between the 2 sexes (Table 3).

Past studies have claimed that devices <5% of body mass have 'minimal' impact on alcid behavior, based on either high return rates, mass loss 'typical' for that species or average chick growth rates (e.g. Croll et al. 1992, p. 348; cited over 20 times as evidence for the '<5% rule'). Some species, such as the small alcids we studied (especially *Synthliboramphus*, Newman et al. 2005), are very sensitive to handling and display negative impacts regardless of the size of the device (Table 1). Nonetheless, even in species with high within-year

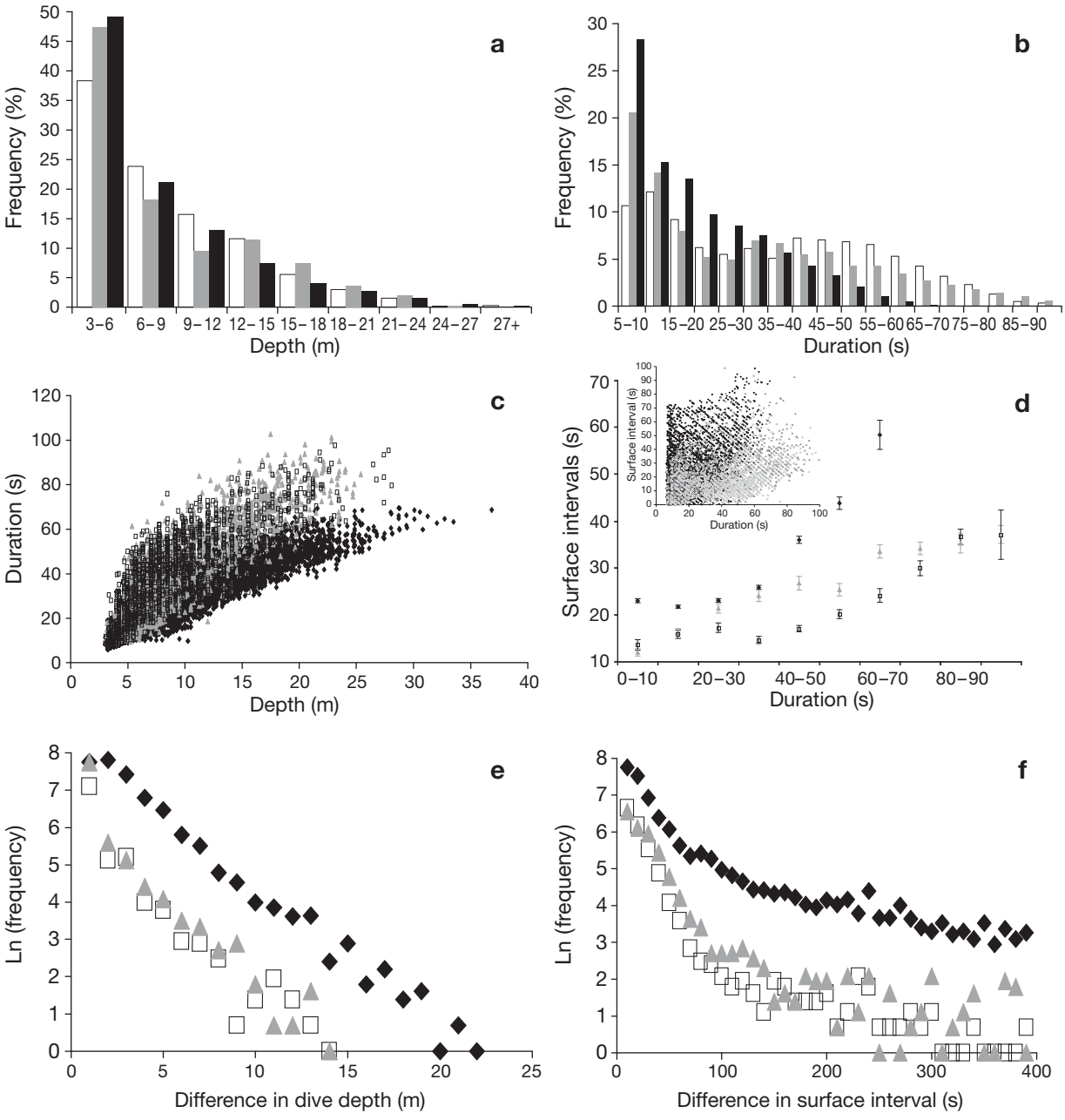

Fig. 1. *Synthliboramphus antiquus* and *Ptychoramphus aleuticus*. (a,b) Frequency histograms for depth and duration of dives, respectively. Cassin's auklets have (c) longer dive duration for a given depth and (d) shorter anticipatory surface pause intervals for a given depth compared with ancient murrelets. Both species showed bout structure following (e) a 1-process model for dive depth and (f) a 2-process model for surface intervals. White: Cassin's auklet (chick-rearing); grey: Cassin's auklet (incubating); black: ancient murrelet (incubating)

recapture rates and low mass loss, easy-to-obtain measures of device effects on the adults, such as mass loss, corticosterone concentration and device retrieval rates, may mask subtle attributes, including time spent feeding, dive behavior and at-sea activity, because of compensation by the mate or because the costs are passed on to the chick (Paredes et al. 2005, Elliott et al. 2007, 2008a, Takahashi et al. 2008). Consequently, devices as low as 1% of body mass may well be impacting measurements of the very parameters they are trying to measure (Table 1), although it is sometimes unclear whether the effects are due to the devices or to handling. We suggest that researchers strive for devices <1% of body mass for alcids, while acknowledging that all devices are likely to impact behavior, in accordance with the uncertainty principle of wildlife biology.

Table 4. Comparison of flying and diving behavior of ancient murrelets and Cassin's aukets with other alcids

Species	Time spent flying (%)	Flights (no. d^{-1})	Time spent diving (%)	Dive shape	No. dives	Max. depth (m)	Source
Ancient murrelet	10.0	21	11.4	V	387	24	Present study
Cassin's auklet	8.1	29	12.7	V,W	305	22	Present study
Dovekie			10.6	V	184	21	Harding et al. (2009)
Rhinoceros auklet			17.0	V,W	261	50	Kuroki et al. (2003)
Razorbill			2.8	V, W	49	36	Paredes et al. (2008)
	13		6.5	V	427	41	Dall'Antonia et al. (2001)
Common murre	3.5		17.1				Monaghan et al. (1994)
	1.4		7.7				Monaghan et al. (1994)
	11.0		14.6				Cairns et al. (1990)
Thick-billed murre	4.6	5	12.6	V, U	160	88	Elliott et al. (2007)
	7.6		16.3	V, U			Falk et al. (2002)
	5.2		11.2	V, U			Falk et al. (2002)
			6.4	W, U	51	110	Paredes et al. (2008)

Physiological parameters, O_2 stores and aerobic dive limits

When our values were combined with values obtained from the literature, myoglobin concentration increased with body mass in aquatic but not terrestrial animals (Lindstedt & Thomas 1994; Fig. 5c). Buffering capacity increased with body mass (t_{16} = 2.69, p = 0.02) and myoglobin levels (Fig. 5d) in aquatic but not terrestrial (myoglobin: Fig. 5d; mass: t_8 = 0.40, p = 0.71) animals. After excluding pinnipeds, which have several adaptations for high blood hemoglobin levels while submerged, blood hemoglobin concentrations decreased with mass in aquatic birds and mammals (Fig. 5b). Marine homeotherms have higher hematocrit, blood hemoglobin and muscle myoglobin content and proton buffering capacity than semi-aquatic homeotherms, which have higher values than terrestrial animals, reflecting the large O_2 stores needed for breath-hold diving (Fig. 5). Similarly, compared to a non-diving charadriiform bird, hematocrit, hemoglobin content and proton buffering capacity was relatively high in both diving auklets (Table 2).

The relatively low myoglobin concentrations found within the skeletal muscles of the 2 small planktivores compared to other vertebrate divers (Fig. 5c) is surprising given the importance of this O_2 reservoir for underwater endurance (Kooyman & Ponganis 1998). Our values were slightly lower than those reported for the pectoralis of other diving alcids (Davis & Guderly 1987, Haggblom et al. 1988, Croll et al. 1992, Enoki & Morimoto 2000), which may have arisen because our breast samples included both supracoracoideus and pectoralis muscle. The high levels of mitochondrial enzymes needed to support high mass-specific metabolic rates (and the corresponding reduction in space available for myoglobin) may underlie the lower myoglobin concentrations (10 g kg^{-1}) found within the flight muscles of the ~200 g planktivorous small alcids compared to those in 980 g murres (14 g kg^{-1}) and 30 000 g penguins (64 g kg^{-1}, Kooyman & Ponganis 1998). A similar explanation could apply to the notably lower skeletal muscle myoglobin concentrations found in star-nosed moles and muskrats (14 g kg^{-1}; MacArthur et al. 2001, McIntyre et al. 2002) compared to larger-bodied divers

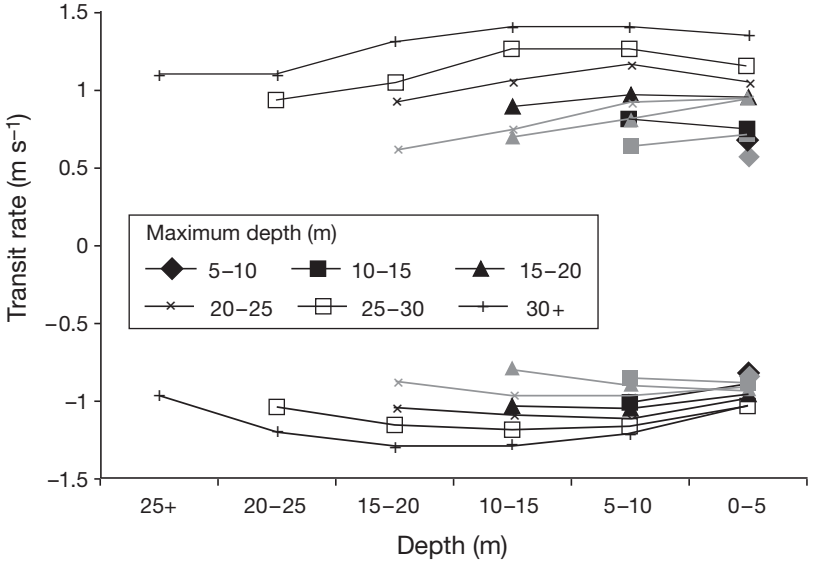

Fig. 2. *Synthliboramphus antiquus* and *Ptychoramphus aleuticus*. Ascent (positive values) and descent (negative values) rates for ancient murrelets (black symols and lines) and Cassin's auklets (grey symols and lines) at different maximum depths. Error bars excluded for clarity. This analysis includes only depths 5 m above maximum depth achieved, and only continuous descents and ascents (no reverses in direction)

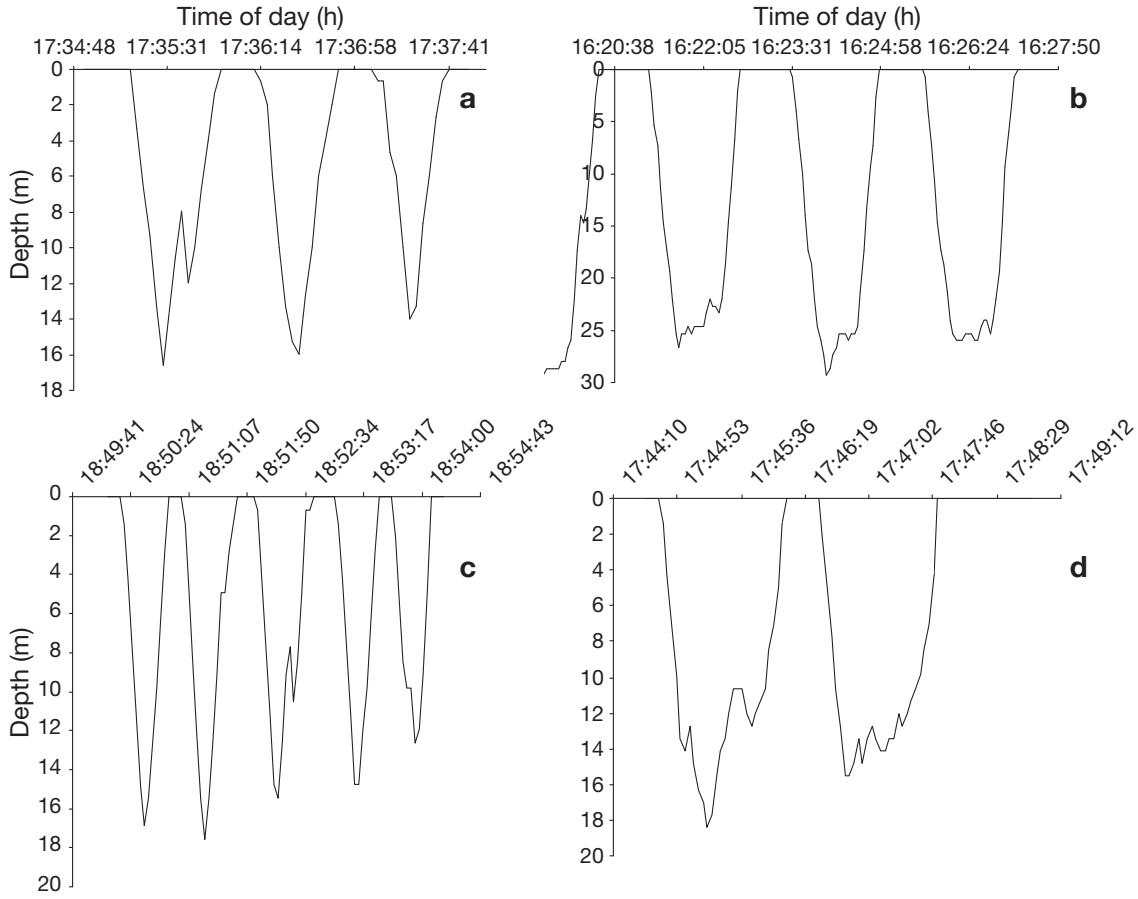

Fig. 3. *Synthliboramphus antiquus* and *Ptychoramphus aleuticus*. Typical dive profiles for (a) incubating ancient murrelets and (b) incubating and chick-rearing Cassin's auklets that subsequently provisioned with (c) fish and (d) krill. Note differences in axis scales

(~60 g kg^{-1} for large toothed whales; Fig. 5c). Conversely, the relatively low myoglobin concentrations found in flying divers (alcids) may instead simply reflect the relatively high mitochondrial volumes needed to support flight (Davis & Guderly 1987, Croll et al. 1992), thus limiting the amount of myoglobin that can be maintained in flight muscle. Because alcid flight muscle is primarily composed of Type I fibers, and Type I fibers have higher myoglobin concentrations than Type II fibers (Ordway & Garry 2004), fiber type cannot explain why alcids have low myoglobin relative to other divers.

Whereas large marine animals, such as pinnipeds and large penguins, have a large proportion of their O_2 stores in their muscle, small birds and mammals do not appear to have this option (Fig. 6). Instead, the majority of O_2 stores are located in the respiratory system and blood (Fig. 6, Table 2), which may lead to increased selective pressure to improve blood O_2 storage and, consequently, high blood hemoglobin concentrations in small aquatic birds and mammals (Fig. 5b). Whether a given small diving species increases blood or respiratory O_2 stores may depend on the depth to which it dives. Shallow-diving ducks have relatively high respiratory O_2 stores, while deep-diving alcids have relatively high blood O_2 stores, possibly because any further increase in respiratory stores would greatly increase buoyancy-related costs when diving to depth (Fig. 6). The high buffering capacity of skeletal muscle in the 2 small alcids (20 to 30% higher than the non-diver; Table 2) is interesting given that buffering capacity increases with body mass in diving mammals because larger animals have higher protein (myoglobin) concentrations (Fig. 5c) and, therefore, may be expected to have a greater number of titratable histidine residues per unit muscle mass. Buffering capacity is also primarily associated with Type II fibers (Hochachka & Mommsen 1983, Nakagawa & Hattori 2002, Abe 2000), so fiber type also cannot explain the discrepancy. Adequate intracellular buffers are critical to ensure optimum pH for glycolysis, the only process of ATP generation in diving animals once O_2 stores are exhausted. Allometric scaling of glycolytic enzymes to mass predicts that small alcids should have a poor abil-

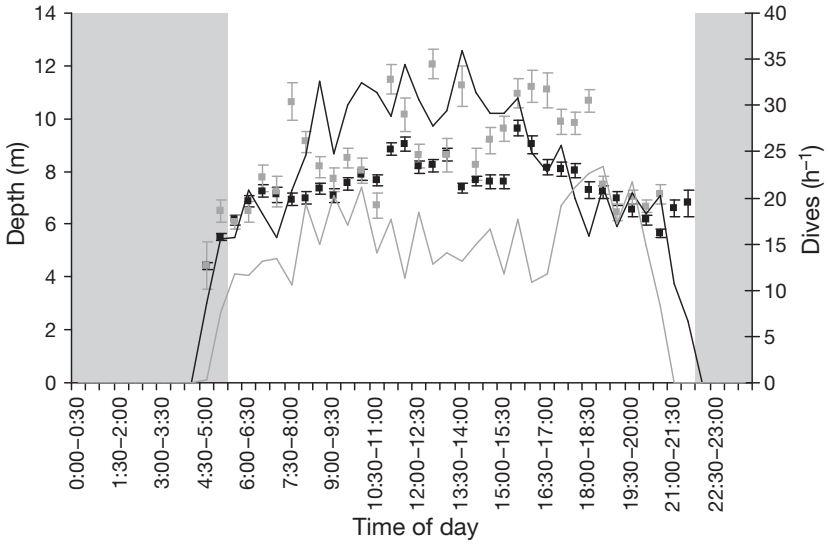

Fig. 4. *Synthliboramphus antiquus* and *Ptychoramphus aleuticus*. Dive depth (squares ± SE) and dives per hour (lines) for ancient murrelets (black) and Cassin's auklets (grey). Note that both variables are highest during midday

ity to utilize glycolysis (Emmett & Hochachka 1981), and a high buffering capacity (more histidines per protein molecule) may be one way in which alcids can enhance glycolysis to extend dives.

Using total O_2 stores shown in Table 2, assuming a metabolic scaling factor of 0.73 and using a diving metabolic rate of 0.93 ml s^{-1} kg^{-1} for murres in a shallow dive tank (~3× basal metabolic rate, Croll et al. 1992, Croll & McLaren 1993), we calculated an aerobic dive limit (ADL) of 39.6 s for murrelets and 39.4 s for auklets. Similar values (~39 s) are obtained if we convert the total O_2 stores of auklets (10.4 ml) and murrelets (11.8 ml) into work (assuming 20.1 J ml O_2^{-1}) and consider the depth achieved (~9 m) if the birds are to descend and ascend on 220 J of aerobic work (Lovvorn 2010, this Theme Section). A depth of 10 m is equivalent to about 39 s (see Fig. 1).

In total, 44% of chick-rearing auklet dives, 36% of incubating auklet dives and 13% of murrelet dives exceeded their estimated ADLs (39 s). Many dives by both murrelets and auklets exceeded their respective calculated ADLs (~39 s). It is unlikely that these small alcids actually routinely exceed their ADL because the surface pause to dive duration relationship for both species (Fig. 1) was weak (cf. Elliott et al. 2008b) and anticipatory, implying that they do not routinely metabolize high levels of lactate at the surface. The calculated ADLs of avian divers are often underestimated (Kooyman & Ponganis 1998, Knower Stockard et al. 2005, Ponganis et al. 2010, this Theme Section). A possible reason for the discrepancy in our case is that diving metabolic rates of free-ranging murres, as measured using doubly labeled water, is less than half the value measured in shallow tanks (which we used to estimate ADLs), likely because low buoyancy costs and enhanced vasomotor responses reduce metabolic rate during deep dives (Niizuma et al. 2007, K. H. Elliott unpubl. data). A 2-fold reduction of the estimated diving metabolic rate would lead to an ADL of ~78 s; few dives for either species exceeded this value. However, alcids engaging in pelagic dives exhibit high activity throughout the dive (Elliott et al. 2009b), so pelagic-diving auklets and murrelets may not show the same degree of reduction in diving metabolic rate as benthic-diving murres; the true ADL of auklets and/or murrelets probably lies somewhere between 39 and 78 s. Experiments measuring O_2 consumption rates and lactate levels for small alcids during diving are sorely needed to resolve this issue, and we use the ADL only as a crude measure for comparing dive behavior.

Foraging behavior

Auklets dove for longer than murrelets, while murrelets dove deeper, meaning that auklets were submerged for 60% longer than murrelets at any given dive depth. Descent rates of both species increased with depth, in accordance with a concurrent reduction in buoyancy (greater acceleration for a constant work per stroke, Lovvorn et al. 1999, 2004), then decreased as the bird approached maximum depth and started searching for prey. Ascent rates decreased with depth, as birds employed buoyancy to return to the surface, and increased with maximum depth, as deep diving birds likely descended with greater air stores and were more buoyant (Sato et al. 2002, Elliott et al. 2007). Descent rates were less variable than ascent rates, possibly because descent rates were maximized to occur in a narrow wingbeat frequency while ascent rates reflected variations in buoyancy. As is the case for murres (Croll et al. 1992, Hedd et al. 2009), and is generally more common in birds than mammals (Kooyman & Ponganis 1998), a high proportion of dives (auklets: 30 to 40%; murrelets: 13%) exceeded their respective estimated ADLs. Higher mass-specific O_2 stores, proton buffering capacity and dive durations for a given surface interval for auklets suggest that auklets are more regularly limited than murrelets by O_2 stores due to the longer dive durations of auklets. There was little difference in shape, depth or duration between individual dives of incubating versus chick-rearing auklets. However, chick-rearing birds spent much more time under-

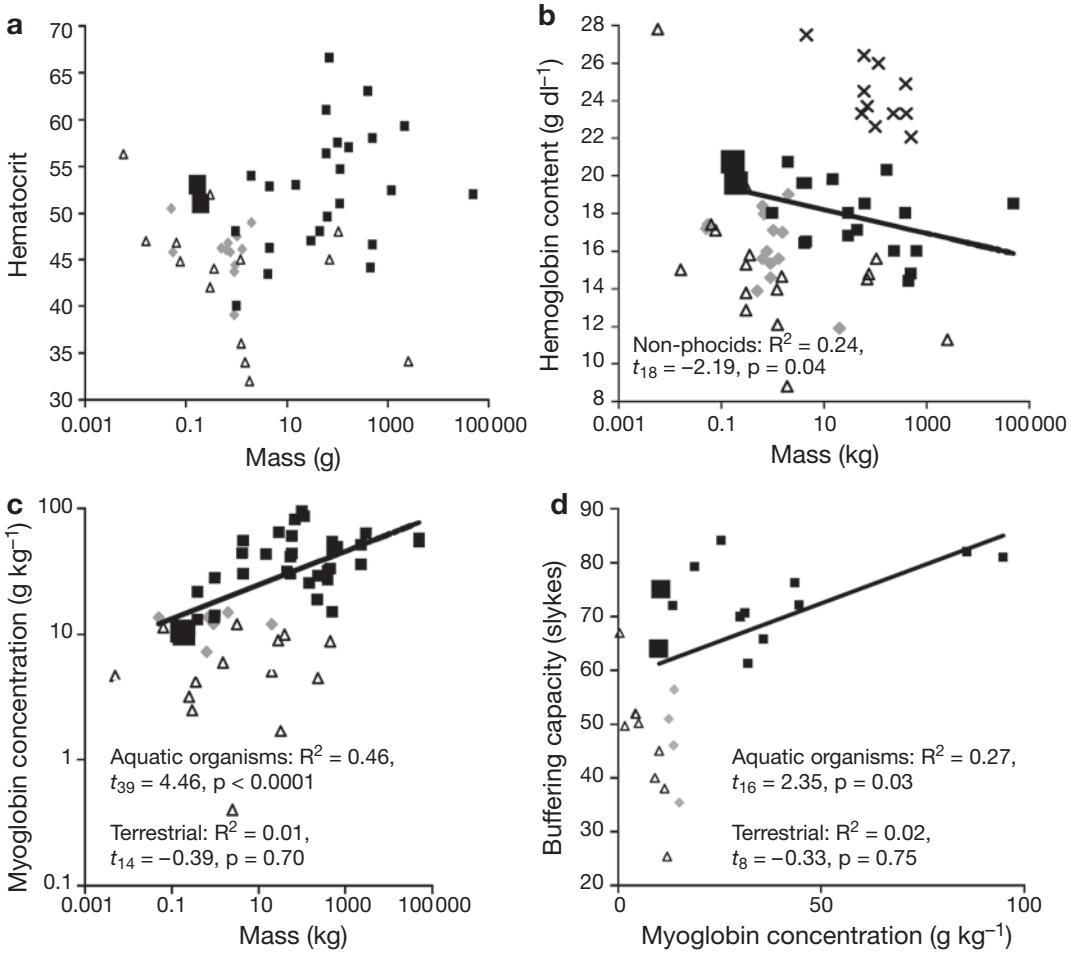

Fig. 5. *Synthliboramphus antiquus* and *Ptychoramphus aleuticus*. (a) Hematocrit, (b) hemoglobin content, (c) myoglobin concentration and (d) proton buffering capacity for semi-aquatic (◆), marine (■) and terrestrial (△) organisms (×: seals, for blood parameters). Regressions are shown for (b) all non-phocid aquatic animals and (c) all aquatic organisms. The large squares represent the 2 small alcids in Table 2. Sources are shown in Table S3 in the Supplement (see www.int-res.com/articles/suppl/b008p221_app.xls)

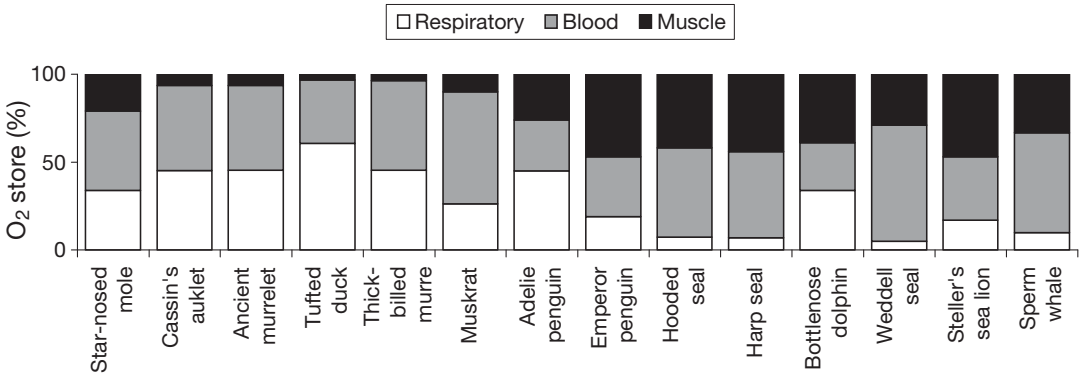

Fig. 6. Oxygen store distribution for a variety of vertebrates

water (dove more frequently, not longer) due to the greater energy demands of chick-rearing.

Neither species dove at night, with diving starting 1 h before sunrise and ending 1 h after sunset (Fig. 4). For auklets, which visited the colony nightly, the absence of night diving might be accounted for by time at the colony. However, most murrelets spent at least 1 night away from the colony during TDTR deployments, hence the absence of night diving presumably relates to limited nocturnal feeding opportunities. Maximum possible radii was 66 km d^{-1} for murrelets and 53 km d^{-1} for auklets; however, as flying was broken into bouts (Table 4),

the maximum distance traveled from the colony was likely much less (Elliott et al. 2009a, Thaxter et al. 2009).

The differences in foraging behavior between auklets and murrelets either represents different foraging tactics for capturing the same prey or differences in prey type, as foraging behavior indicates prey type in other alcids (Elliott et al. 2008a). The dive depths and durations of auklets and murrelets were comparable to those of 150 g planktivorous dovekies *Alle alle*, while dive shape was comparable between dovekies and murrelets (Harding et al. 2009, Table 4). Dive depths and durations were much smaller than for larger-bodied alcids, but total time spent underwater was similar, due to the greater number of dives by the smaller alcids (Table 4). The V-shaped dives of murrelets were also very similar to those associated with other alcids feeding on small fish (Table 4), while the W-shaped dives of auklets were comparable to those associated with *Spheniscus* penguins feeding on schooling krill or other prey (Simeone & Wilson 2003, Takahashi et al. 2004). Auklets provisioning with fish tended to have deeper, V-shaped dives than those provisioning with krill (Fig. 3), and murrelets in Haida Gwaii tended to feed themselves with more fish than auklets (Vermeer et al. 1985), suggesting that the V-shaped dives may be associated with fish and the W-shaped dives with krill. In Haida Gwaii, auklet stomach contents contained 42% copepods, 39% crustacean larvae and 13% krill, while auklet chicks were provisioned with krill and fish (likely sandlance; see also Burger & Powell 1990). Murrelet stomach contents at Haida Gwaii contained 56% krill and 44% fish during mid incubation and 99% fish during late incubation (all of our TDR measurements were in late incubation; Vermeer et al. 1985). Thus dietary information from Haida Gwaii supports the idea that V-shaped dives are used to capture fish (self-feeding, incubating murrelets and auklets provisioning with fish) and W-shaped dives are used to capture invertebrates (self-feeding, incubating auklets and auklets provisioning with krill). To conclude, 2 species of sympatric auklet partitioned their small fish/plankton niche by using different foraging strategies, possibly because they were feeding on different components of the niche (krill vs. fish), and each component was caught in a different manner.

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