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REVIEW

Non-consumptive factors affecting foraging patterns in Antarctic penguins: a review and synthesis

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Abstract Recent research has clearly shown that the fear of predation, i.e. aversion to taking risks, among mesopredators or grazers, and not merely flight from an apex predator to avoid predation, is an important aspect of ecosystem structuring. In only a few, though well-documented cases, however, has this been considered in the marine environment. Herein, we review studies that have quantified behavioral responses of Adélie penguins *Pygoscelis adeliae* and emperor penguins *Aptenodytes forsteri* to the direct presence of predators, and question why the penguins avoid entering or exiting the water at night. We also show, through literature review and new analyses of Adélie penguin diving data, that Antarctic penguins are capable of successful prey capture in the dark (defined here as <3.4 lux). Finally, we summarize extensive data on seasonal migration relative to darkness and prey availability. On the basis of our findings, we propose that penguins' avoidance of foraging at night is due to fear of predation, and not to an inability to operate effectively in darkness. We further propose that, at polar latitudes where darkness is more a seasonal than a year-round, daily feature, this "risk aversion" affects migratory movements in both species, consistent with the "trade-off" hypothesis seen in other marine vertebrates weighing foraging success against predation risk in their choice of foraging habitat. Such non-consumptive, behavioral aspects of species interactions have yet to be considered as important in Southern Ocean food webs, but may help to explain enigmatic movement patterns and choice of foraging grounds in these penguin species.

Keywords Adélie penguin · Apex predator · Emperor penguin · Foraging habitat · Killer whale · Leopard seal · Mesopredator · Predation · Predation fear · Risk balancing

Introduction

It has been noted that "A predictive framework of community and ecosystem dynamics that applies across systems has remained elusive, in part because non-consumptive predator effects are often ignored" (Heithaus et al. 2007: 837), and are difficult to incorporate into trophic models (Wirsing and Ripple 2010). Both studies provide examples of indirect predator effects on potential prey and their habitat use thus to avoid predation. Indeed, as these authors point out, while consumptive, biomass-mediated effects of prey and predator are widely investigated and modeled in ocean ecosystems, behaviorally mediated interactions may be equally important, yet have received relatively little attention, unlike in terrestrial ecosystems. Therefore, a resource-production, bottom-up view overwhelmingly pervades marine ecology due, in part, to the difficulty in acquiring data in the ocean environment and especially behavioral data. Predation events are rarely seen, and as Monod (1991) aptly stated, reiterated by Tremblay et al. (2009: 153): "nothing is more difficult to study than something you cannot see."

One such behaviorally mediated factor, "risk aversion" or fear of predation, and not merely escaping from predators, and how it affects behavior, has become an exciting

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subject of research as re-introduced apex predators expand into ecosystems where they had been absent for most of the period during which modern ecology has developed. With the reintroductions, more than just the cascading effects of renewed top-down forcing pressure on herbivore or mesopredator population size have been measured (e.g., McLaren and Peterson 1994; Prugh et al. 2009); for example, the mere presence of formerly absent apex predators, such as wolves and falcons, even if only infrequently seen by potential mesopredator or grazer prey, has caused these prey to drastically alter their foraging and migratory patterns (Butler et al. 2003; Lank et al. 2003; Ydenberg et al. 2004, 2007). In some cases, changes in these patterns have resulted in repercussions rippling through entire food webs (reviewed in Ripple and Beschta 2004; Heithaus et al. 2008; Wirsing et al. 2008). Prey responses are consistent with a "trade off" in the choice between predation risk versus foraging success. Such risk-averse behavior has been observed in several marine mesopredators, which choose suboptimal foraging habitat thereby reducing predation risk. Examples are green sea turtles *Chelonia mydas* (Heithaus et al. 2007), bottle-nosed dolphins *Tursiops truncatus* (Heithaus and Dill 2002), harbor seals *Phoca vitulina* (Wirsing et al. 2008), pied cormorants *Phalacrocorax varius* (Heithaus 2005), and dugongs *Dugong dugon* (Wirsing et al. 2007) in the face of predation by sharks (and killer whales in the case of the seals); and small shorebirds facing predation by peregrine falcons (*Falco peregrinus*; Ydenberg et al. 2002). In addition, individuals in poor condition have been found to be more prone to taking the risk of foraging where food is plentiful but predation is more likely (seen in the turtles and shorebirds).

Predation by marine mammals is a major component of the life history of penguins, documented to varying degrees (Spellerberg 1975). With respect to Antarctic species, for example, an estimated 5% of a colony population of Adélie penguins *Pygoscelis adeliae* is taken by leopard seals *Hydruga leptonyx* during a summer nesting season, with each seal taking several penguins per day (Penney and Lowry 1967; review in Ainley et al. 2005). This is consistent with relatively low annual survival, <90%, compared with other pelagic seabirds in which >90% is typical (see Schreiber and Burger 2001: Appendix 2). Leopard seals also prey heavily upon emperor penguins *Aptenodytes forsteri*, taking both adults and fledglings from the edge of ice floes and in the water (Wilson 1907; Kooyman et al. 1990). According to the latter authors, given the large body mass of an emperor penguin, a seal needs to take one emperor penguin per day to satisfy energetic needs which, extrapolated to the number of seals and number of days the penguins are present at a colony, equates to a significant take. Emperor penguin annual survival is also estimated to be <90% (Jenouvrier et al. 2009) and, in addition to leopard seals, predation by killer whales *Orcinus orca* is suspected (Mikhalev et al. 1981; Andrews et al. 2008) and consistent with the energetic value of large, fatty prey [see for closely related king penguins *A. patagonicus* (Reisinger et al. 2011; see Discussion)]. Indeed, the survival rate of emperor penguins at Pt Géologie increased dramatically, when in an unintended "experiment" >100 killer whales were removed by whalers from that colony's late-spring (crèche period) foraging area (Ainley et al. 2010a, b). Among some populations of killer whales, e.g., those around the Antarctic Peninsula or subantarctic islands, predation on penguins is common as judged from recent direct observations (Guinet 1992; Pitman and Durban 2010; see also Lauriano et al. 2007).

The behavioral response of penguins to the presence or perceived presence of predators in the immediate vicinity has been long known (e.g., Levick 1914) and quantified (Müller-Schwarze and Müller-Schwarze 1975), and starkly contrasts the behavior of seabirds not subject to intensive aquatic predation (see Grémillet et al. 2005). Herein, we further explore the possibility that fear of predation significantly affects Antarctic penguin natural history patterns and behavior in ways not previously thought to be related to predation (see Lima and Dill 1990 for a general review of behavioral "decisions" with respect to predation in birds).

This paper is largely but not entirely a review of pertinent literature, in which we will integrate review and empirical data to test seven predictions related to penguins' (a) behaviors in response to the presence of predators; (b) behaviors when they are unable to assess whether predators are present (night darkness); (c) capabilities to forage successfully in the dark; and (d) long-range, seasonal movement patterns as predator avoidance and/or avoidance of situations in which predation risk cannot be assessed. Penguins' capabilities to forage in the dark were assessed by deploying time-depth-recorders with light sensors. In the end, on the basis of our findings, we propose that penguins, like other marine mesopredators, demonstrate a balancing of predation risk with foraging success in their behavioral patterns and choice of habitat.

Methods

Penguin literature

We delved into the literature related to penguin foraging activity, foraging success, and spatial distribution by time of day (level of darkness) and in different seasons. We were particularly interested to note patterns that could be construed as predation avoidance, as detailed in the text.

Diving behavior of Adélie penguins

We determined foraging capabilities relative to light levels by equipping 65 adult birds, breeding at capes Crozier and Royds, Ross Island, with MK7 time-depth-recorders (TDR; Wildlife Computers, Redmond, WA 98052, USA) between December 2000 and January 2002 (i.e., two Dec–Jan breeding seasons). These instruments recorded depth and light every second; TDRs weighed 31.3 g (<1% of a 4 kg penguin), measured 1.1 × 2.0 × 8.5 cm (1.0–1.6% of a bird's cross-sectional area). Details on attachment procedures have been provided previously (Ballard et al. 2001).

The tags' light sensors measured irradiance with unspecified scale. We compared irradiance measurements from a light sensor on a sample tag with those from a radiometer (PUV-2500; Biospherical Instruments, San Diego, CA USA) lowered to 35 m and to 90 m in two locations with differing ice cover. Light intensity in the PAR band (photosynthetically available radiation; 400–700 nm) from the radiometer was converted to illuminance (lux) assuming 1 $\mathrm{Wm}^{-2} \approx 4.2$ μEinsteins $\mathrm{m}^{-2}\,\mathrm{s}^{-2}$ at 550 nm (Lalli and Parsons 1993; McCafferty et al. 2004). Results showed that irradiance measurements from the two instruments were highly, though not perfectly correlated [$P < 0.0001$, $\beta = 0.049 \pm 0.0005$, $r^2 = 96.2\%$; i.e., tag light sensor output × 0.049—8.962 ≈ log(PAR score)]. To aid in comparability with other studies, we used this equation to predict equivalent PAR irradiance for all tag measurements, and converted to illuminance (lux) by multiplying by an arbitrary but convenient luminous efficacy of 100 lumens/W (following McCafferty et al. 2004). Using these materials and methods, 0.10 lux was the effective lower limit of our sampling capability—all illuminances of ~0.10 and less (including zero) would appear the same in our data. We were not able to calibrate for possible inconsistencies in light sensitivity among light sensors used, but we believe this would have minimal effect in this study because all instruments shared roughly the same reading (117–120 unspecified units) in a completely dark room.

Diving data were processed using custom software written by GB (following Lescroël et al. 2010). The program corrected the record baseline depth and computed several individual dive parameters including maximum dive depth, bottom time (time spent at >60% of maximum depth), descent rate, ascent rate, dive shape, and number of undulations >1 m (i.e., changes in underwater swimming direction from ascent to descent) to classify dives into three types: foraging ("U"-shaped), exploratory ("V"-shaped), and other (Chappell et al. 1993; Schreer et al. 2001; see also Ropert-Coudert et al. 2001). A foraging dive had at least one undulation (a change of swimming direction from down or flat to up and then back to down; Zimmer et al. 2010). For our purposes in this paper, we evaluated only foraging dives that resulted in a maximum depth of ≥10 m and duration ≥30 s. Shallower and shorter-time-duration dives would be affected by penguins' getting deep enough just to get under ice floes and pressure ridges, and thus causing confusion in interpretation of the signal. The program also summarized mean light as recorded by tags between 4.5 and 5.5 m and mean light during the bottom phase for each foraging dive. We did not correct for any potential bias in light sensor measurements associated with dive angle (steeper dives could be expected to record lower light levels) because there was relatively little variability in the descent rates in the dives that were included in the analyses (95% CI: 1.32–1.33 m/s, $n = 21{,}919$), which we assume would equate to very little bias. We used number of undulations as an index of foraging success (Ropert-Coudert et al. 2001; Bost et al. 2007; Lescroël et al. 2010).

Analyses of dive data

To evaluate predictions, we used two generalized linear mixed models (GLMMs) fitted using maximum likelihood, with individual treated as a random effect, allowing us to use unbalanced repeated measures (Bolker et al. 2009; Tables 1, 2). We included colony and year as fixed, categorical effects since we expected these to influence the dependent variables (maximum foraging depth and foraging success) as well, and not including these factors would be expected to yield non-normal model residuals. For the foraging success model, we also checked the interaction between the amount of light at the bottom of a dive and maximum foraging depth to assess whether the effect of light level on foraging success was consistent at different depths. Two factors negatively affecting light availability at depth that we were not able to measure were (1) the intense phytoplankton bloom sometimes prevalent in surface waters of the study area (DiTullio et al. 2000) and (2) the fact that many dives were under sea ice. All statistical tests were performed using STATA (v.10.1; Stata Corp. 2008), and model residuals conformed to expectations of normality. Means are presented ±SE.

Results

Predictions relating penguin behavior to the presence of predators

Prediction 1: penguins display behaviors consistent with minimizing exposure to predators

The ways in which Adélie penguins behave, sensing that leopard seals are or could be present, was quantified by

Müller-Schwarze and Müller-Schwarze (1975) who worked where there was 24-h daylight. The penguins' behaviors in this situation are as follows:

- Never stay in the water longer than necessary;
- Keep to ice floes;
- Across continuous ice, stay to the ridges, and avoid thin ice;
- If on thin ice, and a leopard seal is beneath, remain motionless;
- Stay alert—single penguins turn their heads more often than those in flocks;
- When a flock in the water encounters a seal, flee in multiple directions;
- When in the water, upon encountering a seal, quit porpoising, and swim continuously;
- When at the beach or ice edge, watch for flocks safely swimming;
- In the vicinity of danger, refrain from vocalizing;
- Divert movement away from a sleeping seal on beach or ice.

Müller-Schwarze and Müller-Schwarze also showed that penguin comings and goings were more frequent during periods when leopard seals tended to be hauled out on floes, sleeping. At locations such as Cape Bird, Ross Island, where the landing beach stretches 5 km, if a penguin comes ashore at the "wrong" end of the beach, instead of directly opposite the colony, it will walk the 5 km rather than return to the ocean to cover the distance several times more rapidly.

Confirming that at least some of these behaviors extend to emperor penguins (though we think that all apply), with respect to rules 1, 2, and 8 above, on 15 November 2008 at Cape Royds, we observed 12 emperors vigorously fleeing the water when 7 "type-B" killer whales (cf. Pitman and Ensor 2003) appeared; the penguins remained on the fast ice, back from the edge, for as long as the whales were in the vicinity (10 h). In addition, in regard to the Müller-Schwarzes' observations of inversely complementing activity cycles, penguins versus their predators, Ainley et al. (1984) reported that emperor penguins at sea (to a lesser degree Adélies, too) forage most intensively during that part of the day when leopard seals are more likely to be resting on ice floes.

In addition to these predation-avoidance behaviors, penguins also avoid lingering in the "danger zone" (e.g., waters near to where penguins exit and enter colonies), e.g., by "bathing" several hundred meters beyond (cf. Kooyman 1965; Penney and Lowry 1967; Ainley 1975). At small colonies, where leopard seals are rarely present (due to lack of predatory opportunity, see Ainley et al. 2005), penguins bathe immediately adjacent to the beach (Ainley, personal observation).

Prediction 2: penguins modify their behavior relative to their ability to determine predator presence

A number of papers report that, at latitudes where there is a daily day–night cycle, most penguins, including Adélies and emperors, avoid entering or leaving the water during dark, i.e., crossing the "danger zone" where predators concentrate near colony beaches or ice edges (Kirkwood and Robertson 1997a, b; Cannell and Cullen 1998; Jansen et al. 1998; Takahashi et al. 2003; Lescroël and Bost 2005; Nesterova et al. 2010); for example, although they do not forage at night (Wilson et al. 1993), when chick-provisioning Adélie and other penguin species leave the beach in the late afternoon, they have insufficient time to fill their stomachs before darkness falls and will delay return until the next morning. A similar behavior pattern is seen also at sea in the pack ice. In a census study conducted throughout the entire Ross Sea, where emperor penguins concentrated in summer near the very productive Ross Sea Shelfbreak Front (Ainley and Jacobs 1981), they were in the water only during 06:00 to 17:00 h, sitting on ice floes in the darker part of the 24-h period; Adélie penguins exhibited a broader foraging period but also were on the ice when it was darkest (Ainley et al. 1984). During a winter cruise (late May) to the same region, emperor penguins were seen in the water only when there was maximum light, and again mainly in the very productive Shelfbreak Front (van Dam and Kooyman 2004).

We propose that avoiding movement into or out of the water in the dark is a response to not being able to judge that it is safe to do so.

Predictions related to foraging

Rates of prey ingestion relative to light levels have been studied for at least seven penguin species: Adélie, emperor, king, African *Spheniscus demersus*, gentoo *P. papua,* chinstrap *P. antarctica* and little penguin *Eudyptula minor* (Wilson et al. 1993; Cannell and Cullen 1998; Bost et al. 2002; Zimmer et al. 2008). In all cases, prey ingestion was severely reduced, even nil, during the dark part of any 24-h period. See also Miller and Trivelpiece (2008), who assessed chinstrap foraging relative to sunrise and sunset, rather than to actual measures of light; and Zimmer et al. (2008), who assessed emperor penguin foraging relative to light levels modeled from insolation, though without consideration of ice cover nor turbidity. Indeed, both ice cover and phytoplankton blooms can dramatically alter light penetration into the ocean (Arrigo et al. 1998). We investigated this relationship to darkness further, using four predictions related to penguins' avoidance of low-light (night) conditions during foraging, and consistent with risk minimization rather than reduced foraging success. During the study, penguins were bringing back large food loads and chicks were growing normally (Ainley et al. 2004, 2006).

Prediction 3: illuminance of foraging dives—a darkness threshold exists below which Adélie penguins will not forage

Of the 21,919 foraging dives that we recorded, 50% averaged illuminance levels of <11 lux and 97% averaged <400 lux, which is the illuminance equivalent to the high end of civil twilight (geometric center of sun between the horizon and 6° below horizon; Bond and Henderson 1963). The majority of dives (82%) did not go below 1 lux, though 35% averaged 3.4 lux or less (lower end of civil twilight; Fig. 1). Therefore, Adélie penguins are willing to forage in the dark, at least as defined from a human perspective, and we were unable to find a darkness threshold using our methods. To add perspective, note that the 1% light level ranges from 13 to 53 m in the southwestern Ross Sea during summer as a function of the plankton bloom (Arrigo et al. 1998). We do not know how 1% light translates into lux, but seemingly this is very dark. Adélies in our study often foraged much deeper than this, sometimes under ice and in waters experiencing a bloom.

Prediction 4: Adélie penguin foraging dive depth is affected by available light near the surface

Light available at 5 m ranged from 16.7 to 4,994 lux (mean 1,169 ± 6.4), and maximum foraging depth ranged from 10 to 113.5 m (mean 43.08 ± 0.13). Maximum foraging depth was positively related to light level (lux) at 5 m. However, this effect, though statistically significant, was relatively small: every increase of 100 lux at 5 m increased predicted foraging depth by just 0.26 m (Table 1). Given the measured range of available light at 5 m, this translates to a ~13 m effect on foraging depth. Colony and year were also important determinants of maximum depth, with Cape Royds penguins diving 23 m shallower, on average, than Cape Crozier penguins, and Cape Bird penguins diving 10 m shallower than Cape Crozier penguins (Table 1).

Predictions 5 and 6: a positive relationship exists between foraging success and light availability at the bottom of dives, as well as the amount of light available at the surface

Foraging success ranged from 0 to 14 undulations (mean 3.78 ± 0.015; $n = 21{,}194$ dives, 65 individuals). Average illuminance at the bottom of dives ranged from 0.097 to 685.71 lux (mean 63.63 ± 0.76). Foraging success was slightly higher at lower light levels during the bottom phase (0.23 more undulations for every reduction of 100 lux) and higher at greater depths (3.4 more undulations for every 10 m more depth; Table 2). The interaction between bottom light and depth was negative ($Z = -9.30$, $P < 0.0001$, $\beta = -0.00012 \pm 0.00001$), meaning, for example, that the deeper the dive, the less the negative effect of light, and the shallower the dive, the greater the negative effect of light on foraging success.

The effect of light availability at 5 m (surface) on foraging depth was statistically significant but inconsequentially small: a 100 lux decrease in light at 5 m was projected to increase foraging success by 0.007 undulations. Penguins were more successful at Cape Crozier than at Cape Bird and there was no effect detected when comparing Royds and Crozier or comparing 2000 and 2001.

From these results, we conclude that Adélie penguins forage successfully in dark conditions. If Adélie penguins were not limited by darkness, why they did not forage even deeper in our study probably has to do with the depth at which they encountered prey. Adélies are known to dive to 175–180 m (Whitehead 1989; Watanuki et al. 1997).

Emperor penguin dive behavior with respect to darkness

We had no direct observations of our own for emperor penguin diving capabilities relative to light, but the literature is rich with analyses relevant to our paper. Though they typically forage at 50–100 m (like Adélies), emperor penguins at times dive to depths of over 500 m (i.e., quite dark; Kooyman and Kooyman 1995). Such deep dives are made only between 05:00 and 19:00, which is the brightest part of the austral day at 74°S and, accordingly, Kooyman and Kooyman (1995), working where there was 24-h daylight, speculated that such deep dives would not be made in the darkness of winter. Studies farther north (67°S) found that, during winter, emperor penguins occasionally foraged to depths >400 m, though they did this (and all diving) only during the brief period of winter daylight at those latitudes (Kirkwood and Robertson 1997a, b).

Predictions related to balancing predation risk with prey availability through habitat choice

Prediction 7: Adélie penguins' non-breeding season movements balance presence where prey availability is highest and predation risk is lowest

It was confirmed quantitatively by Ballard et al. (2010a) (see also Ainley et al. 1993; Fraser and Trivelpiece 1996) that Adélie penguins spend the winter where the pack ice is

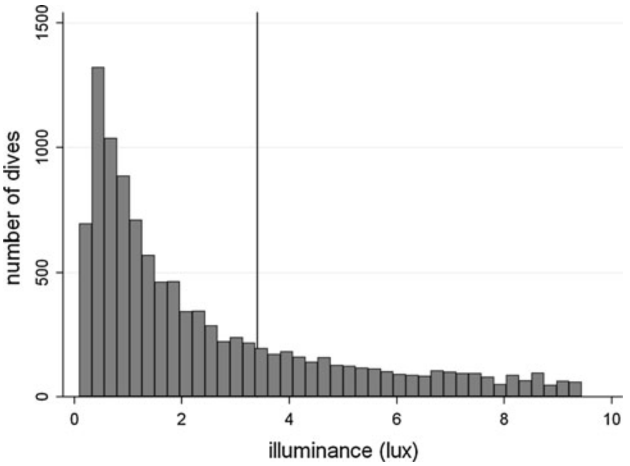

Fig. 1 Distribution of mean illuminance during the *bottom* (presumed foraging) phase of Adélie penguin foraging dives for the *darker* 50% of the full sample of 21,119 dives made by 65 individuals, 2000–2001; *vertical line* at 3.4 lux indicates *darkness* from a human perspective (i.e., edge of civil twilight; Bond and Henderson 1963)

sparse enough to allow access to the sea, i.e., usually not >80% cover. During a given 24-h period during winter, however, they are in the water only in the brightest part of the day (Fraser and Trivelpiece 1996). This is consistent with the idea that Adélie penguins can forage at very low light levels, yet they choose not to initiate swimming or foraging in the dark. Also, they do not winter south of where there is no light (i.e., south of the latitude of zero civil twilight, <3.4 lux; Ballard et al. 2010a).

We contend that this winter movement away from darkness is a way to continue to dwell in an environment where penguins can assess whether or not they risk predation while foraging. Indeed, Adélie penguins of the Ross Sea (the southernmost breeding penguins), during their fattening to regain condition and to sustain their annual post-breeding molt (requires fasting), forage in waters overlying the outer shelf and Shelfbreak Front. These are by far the most productive waters in the region, indicated by immense numbers of birds, whales, seals and their prey (Ainley and Jacobs 1981; Ainley 1985; Ainley et al. 2010a; Ballard et al. 2010b). After molt, they remain in that highly productive zone until darkness arrives and they move north to less productive waters (Ballard et al. 2010a).

Prediction 8: emperor penguins' non-breeding season movements balance presence where prey availability is sufficient but more importantly where prey risk is lowest

During the breeding period, despite (a) the likelihood that concentrating foraging in a confined area near to colonies increases interference competition (large numbers of individuals diving repeatedly in confined areas; see Ballance et al. 2009), (b) the limited amount of daylight available when foraging is possible, and (c) the fact that emperor penguins are capable of making very long foraging trips (Wienecke et al. 2004), nevertheless most breeding emperor penguins forage near breeding colonies. The habitat exploited is the highly productive waters overlying the continental shelf, accessed by diving into tide cracks and relatively isolated polynyas (Ancel et al. 1992; Wienecke and Robertson 1997; Burns and Kooyman 2001; Wienecke et al. 2004; Zimmer et al. 2007). The likelihood that interference competition for food is greatly increased is balanced by the lack of any predators, seals or killer whales, which cannot hold their breath sufficiently long to penetrate into those areas. At the same time, however, a few breeding individuals demonstrate the capability of foraging over the productive Shelfbreak Front and beyond, farther from the colony, without compromising breeding success (Wienecke et al. 2004) but possibly increasing predation risk. Males in particular, after fasting during courtship, laying, and incubation (2–3 months), are in poor physiological condition once relieved by females at the time chicks hatch. Males experience especially high mortality at this time, especially under conditions of reduced sea ice (Barbraud and Weimerskirch 2001; Jenouvrier et al. 2009). Without food web data but consistent with a resource exploitation theme, these authors hypothesized that the elevated mortality was due to starvation from low food availability. However, as detailed below, we contend that high mortality of males described by these authors seems like a classic case of high risk-taking induced by compromised condition (Anholt and Werner 1995; Heithaus et al. 2007).

When recovering post-breeding condition and to fatten before the molt, at a time when the disappearance of protective fast ice has exposed them to greater predation risk, emperor penguins of East Antarctica make a trip of 3–6 weeks to forage far to the north, up to 61°S (Wienecke et al. 2004; Zimmer et al. 2007), i.e., well north of the highly productive Shelfbreak Front and those waters that lie south of the Southern Boundary of the Antarctic Circumpolar Current (sbACC). Crossing the sbACC they move into oligotrophic waters, where food is relatively scarce (see Tynan 1998; Arrigo et al. 1999; Nicol et al. 2000; Smetacek and Nicol 2005; Smith and Comiso 2008). In the case of Ross Sea emperor penguins, in contrast, they travel to the Shelfbreak Front in the eastern Ross Sea and Amundsen Sea, where the pack ice is very heavy year round (Kooyman et al. 2004). During these trips, adults are constantly on the move rather than remaining in confined areas as when foraging in winter (breeding) over the shelf (see Wienecke et al. 2004; Zimmer et al. 2007). They then return to molt on pack ice near the coast (Kooyman et al. 2004; Wienecke et al. 2004).

Table 1 Factors influencing maximum foraging depth for 65 Adélie penguins (21,194 dives), 2000–2001, Ross Island, Antarctica

Variable	Coefficient	Std. Err.	Z	$P > z$	95% conf. interval	
a						
Light at 5 m	0.0026	0.0001	20.16	<0.001	0.0024	0.0029
Colony = Royds	−22.68	3.02	−7.50	<0.001	−28.61	−16.75
Colony = Bird	−9.76	4.33	−2.25	0.024	−18.26	−1.26
Year = 2001–2002	1.95	3.84	0.51	0.612	−5.58	9.47
Intercept	43.35	2.22	19.53	<0.001	39.00	47.70
b						
Random intercept SD ($\sqrt{\psi}$)	9.89	0.88			8.31	11.76
Level 1 residual SD ($\widehat{\sqrt{\theta}}$)	14.40	0.07			14.27	11.76
Within ID correlation (ρ)	0.32	0.04			0.25	0.40

Results from mixed effects generalized linear model with individual treated as random effect. Statistics for fixed effects (*a*) compared with random effect (*b*)

Table 2 Relationship between light availability and foraging success for 65 Adélie penguins (21,194 dives), 2000–2001, Ross Island, Antarctica

Variable	Coefficient	Std. Err.	Z	$P > Z$	95% conf. interval	
a						
Light at foraging depth (lux)	−0.0023	0.0002	−13.61	<0.001	−0.0026	−0.0019
Light at 5 m (lux)	−0.00007	0.00002	−3.76	<0.001	−0.0001	−0.00003
Maximum depth (m)	0.034	0.001	29.13	<0.001	0.032	0.036
Colony = Royds	−0.32	0.21	−1.48	0.14	−0.73	0.10
Colony = Bird	−0.82	0.30	−2.73	0.006	−1.40	−0.23
Year = 2001–2002	0.29	0.26	1.09	0.275	−0.23	0.80
Intercept	2.50	0.16	15.37	< 0.001	2.18	2.82
b						
Random intercept SD ($\sqrt{\psi}$)	0.67	0.06			0.56	0.81
Level 1 residual SD ($\widehat{\sqrt{\theta}}$)	1.94	0.01			1.92	1.96
Within ID correlation (ρ)	0.11	0.02			0.08	0.15

Results from mixed effects generalized linear model with individual treated as random effect; the dependent variable is undulations at the bottom of dives. Statistics for fixed effects (*a*) compared with random effect (*b*)

Finally, it has recently been shown that emperor penguin fledglings also exhibit a northward excursion on their "maiden trip", crossing the sbACC and in some cases visiting the APF or north (to nearly 54°S) but returning within several weeks (by about March) to forage in Shelfbreak Front waters (Kooyman and Ponganis 2008; Wienecke et al. 2010). Interestingly, Wienecke et al. (2010) indicated that fledglings, while making the outward journey through the richest foraging habitat, experience a very high mortality (~30%); the mortality rate was 20% among fledglings on their outward journey in the Ross Sea study (Kooyman et al. 1996; Kooyman and Ponganis 2008). Once the fledglings reach northern waters, mortality is much reduced (Wienecke et al. 2010).

Discussion

In this study, we found that once in the water, Antarctic penguins are capable of foraging successfully in the darkest depths, yet will not enter nor exit the water during night. During those transitions, they are most susceptible to predation. The avoidance of such risk forces Adélie penguins to move away from southern areas that have no light during winter. In the case of emperor penguins, without the protection of fast ice, which has broken up by later summer, they migrate away from highly productive waters to forage in waters that are relatively depleted of prey.

In marine ecosystems, it has been shown for several mesopredators—dolphins, dugongs, cormorants, sandpipers, and sea turtles—that their habitat use balances predation risk and foraging success, a phenomenon well known in terrestrial systems (reviewed in Wirsing and Ripple 2010). Further, it has been found that individuals in poor body condition take risks by opting for habitats where food is more available, but top predators are more abundant as well and vice versa for individuals in good condition (Ydenberg et al. 2002; Heithaus et al. 2007; Wirsing and Ripple 2010). Fear of predation, or risk avoidance, is the factor controlling these patterns, and it appears from our review and analysis that this is likely the case to explain the patterns we reported in Antarctic penguins.

Penguin foraging

We found that Adélie penguins forage at very low light levels, and that the amount of light somewhat positively affects depth of foraging, but negatively (weakly) affects foraging success. This implies that there is top-down structuring of prey availability in this system, i.e., the penguins regularly chase their prey to the limits of their physiological capability to capture it. This prey-depletion effect has been described previously for the study system in the horizontal dimension (Ainley et al. 2004, 2006) as well as in the vertical dimension (Ballard 2010; Lescroël et al. 2010). In any case, apparently penguins can cope or even forage more successfully with very low light once they are in the water. It should be noted that, while we have done our best to present the data in a way most comparable with other studies, it is quite possible that the illuminances we and others have reported do not correspond perfectly with illuminance from a human or a penguin perspective, and thus, what we interpret here as “dark” is somewhat arbitrary. Furthermore, underwater illuminance levels vary substantially by wavelength and light angle (time of day). Thus, our results should be confirmed with light sensors that are explicitly calibrated to record illuminance from a penguin’s perspective, which would also require that penguin eye sensitivity be thoroughly investigated.

The potential prey of Adélie penguins and other air-breathing predators usually move closer to the surface during dark(er) periods (Gliwicz 1986, specifically in the case of silverfish in the Ross Sea when coastal mountains shade sunlight from the ocean: Fuiman et al. 2002). Presumably, this is the reason that a large proportion of seabirds feed mainly at night (e.g., Spear et al. 2007), including most Antarctic species of the family Procellaridae (Ainley et al. 1984, 1992). Facilitating the behavior is the fact that the myctophid fish and krill consumed by these predators, including Antarctic species in winter, glow in the dark (Ainley et al. 1992; Martin 1999). Other diving species, such as Antarctic seals, take full advantage of the diel movement of prey, making shallow, less energetically demanding dives when it is darkest, but penguins only do so in a limited way (cf. Croxall et al. 1985; Wilson et al. 1993; Gelatt and Siniff 1999; Fuiman et al. 2002). Why the difference? Moreover, despite penguins’ frequent dives into dark conditions, and where, like seals, penguins may capture back-lit prey silhouetted against the lighter surface (Davis et al. 2004), i.e. “shadow theater” (Zimmer et al. 2008), given the choice, penguins do not enter the water at lowest light levels. If they are in the water then they remain there but do not forage. Why, too, this difference from seals?

Wilson et al. (1989), concluding that penguins were visual predators, stated that “consistent changes in penguin depth utilization according to time of day would indicate a primarily light-dependent foraging pattern” (see also Cannell and Cullen 1998; Bost et al. 2002). Subsequent research supplemented this idea from the prey’s perspective. Wilson et al. (1993) essentially proposed that prey should remain in the darkness to the greatest extent possible to avoid predators, and that the depth of this would change according to hour of the day (see also Clark and Levy 1988). Information available at that time seemed to indicate that krill, for instance, could not dive deeper than ~100 m due to oxygen limitation with depth. Since then, however, it has been shown that krill and silverfish occur throughout the water column, even to depths $\gg$500 m (e.g., Fuiman et al. 2002). At least in the case of crystal krill *Euphausia crystallorophias*, a major prey item of Adélie penguins in the Ross Sea, its main predator are fish not penguins (La Mesa et al. 2004) and silverfish have no depth or light constraints (Eastman and Lannoo 2011).

Light dependency when foraging is somewhat supported by our finding that Adélie penguins dove slightly deeper when there was more light available near the surface (cf. Bost et al. 2002 for a similar pattern in king penguins). Our results indicating that greater foraging success is reached at lowest light levels at depth also potentially support the proposal by Wilson et al. (1993) that prey are hiding or being chased to the limit of Adélie penguins’ visible acuity. It is also possible that darkness improves penguin foraging capability, for example, by providing cover so that prey cannot observe them, or by enhancing bioluminescent prey visibility (see again Clark and Levy 1988). It is also possible that they simply did not need to go deeper (which is more energetically expensive) since an adequate amount and quality of prey was encountered at shallower depths.

Still lacking, therefore, is a parsimonious explanation as to why penguins remain away from the colony, do not forage, and do not enter the water in darkness (Wilson et al. 1993). We propose that the reasons behind these behaviors, given penguin performance relative to various of our predictions, are related to the fact that, being visually oriented, penguins must see that it is safe before diving into and moving about in the ocean, but in the dark they cannot assess safety. This is important because, unlike most other seabirds (e.g., Grémillet et al. 2005), penguins, as mesopredators, are at times an important prey for certain apex or near-apex predators, such as seals, killer whales, and sharks. Also, other seabirds, which, like penguins, must leave their young at the colony in order to forage for a long day or multiple days at sea, use darkness to come and go at the nest as a strategy to reduce predation by terrestrial or aerial predators. During this "transitional" period of heightened anxiety, the penguins' reluctance to proceed in the dark is, thus, in stark contrast to that which is well known among petrels and small alcids. Only the little penguin comes ashore at night, but it is very small and actually breeds extensively in areas where there are terrestrial predators (thus, it needs to avoid being seen during day).

Penguin longer-range movements

Risk-averse behavior may have further large-scale implications, given that Antarctic penguins have to deal with predators year round (e.g., winter: Gill and Thiele 1997; van Dam and Kooyman 2004; summer: see references in the Introduction). Leopard seals dive to 300 m and killer whales forage to 450 m (Nordøy and Blix 2009; Baird et al. 2003), and thus certainly can cope with the dark. Leopard seals occur in the Antarctic pack ice year round (which extends to the sbACC in winter), but less is known about killer whales. In the case of the winter observations reported by Gill and Thiele (1997), their photograph was of the fish-eating, resident, "ecotype-C" killer whale, rather than a type-B or A (mammal/penguin predators; Pitman and Ensor 2003; Pitman and Durban 2010). Nevertheless, to an emperor penguin, it is likely that any killer whale seen would cause anxiety (see below). For Adélie penguins needing to assess safety when at sea means a constraint on how far south they can spend the winter; for emperors, which breed during winter with a small portion of colonies below the zone where at least twilight exists in mid-winter, it possibly could mean a constraint to how far south they can breed in any significant numbers. Adélie penguins require sunlight by which to undertake long-distance navigation (reviewed in Ainley 2002, pp. 35–37), though local movements are possible in twilight. Nothing is known of emperor penguin navigational abilities, although certainly individuals at the southernmost colonies can find their way; king penguins can find their way within colonies at night (Nesterova et al. 2010). Currently, just seven of 38 emperor colonies exist south of 75°S, all of them among the smallest for the species (Woehler 1993; Fretwell and Trathan 2009). This is about 250 km south of latitudes where twilight occurs in winter (Ballard et al. 2010a). However, emperor penguins' unparalleled ability to fatten and fast allows non-incubating/non-brooding members of pairs to make foraging trips reaching 60–500 km from the colony while the mate tends to the egg or chick (Wienecke and Robertson 1997; Zimmer et al. 2007). The southernmost colonies, therefore, are within reach of adequate light for avoiding predation while foraging, as surmised by van Dam and Kooyman (2004).

Of great interest but to date difficult to explain are the northward trips made by emperor penguin adults in late summer (January–February) in order to recover condition from breeding and to fatten before molting, eschewing productive waters of the Antarctic Shelfbreak Front or even those south of the sbACC. These frontal areas are far more productive than waters to their north. During this period, recently fledged juveniles make a similar trip to these relatively unproductive waters north of the sbACC. As testament to their relatively low food availability, the closely related congener, king penguins, forage in these waters year round but exhibit very slow chick growth and require 15 months to complete one breeding cycle (Williams 1995). The emperor penguins' return to productive shelfbreak waters to fatten prior to breeding or in the case of juveniles to continue to develop. Remarkably, and contrary to Zimmer et al. (2007: 229, 241—such trips "…argue for particularly profitable oceanic feeding areas"), we contend that emperor penguins are choosing the least productive portion of the Southern Ocean during this period. In contrast, Adélie penguins remain as long as possible in productive waters, especially those of the Shelfbreak Front, until darkness sets in and they move north (Ballard et al. 2010a).

In the case of emperor penguin fledglings, Kooyman and Ponganis (2008) were at a loss to explain their short-term movement away from highly productive areas. On one hand, it could be an attribute selected to respond to high levels of inter- and intraspecific competition for food (see e.g., Burns and Kooyman 2001). On the other hand, the movement to less productive areas is consistent with a selected "trade-off" response to reduce predation. Fledglings may be genetically instilled with a "risk-averse" sense, but adults might well remember, i.e., have learned from, harrowing experiences encountered upon their maiden journey away from the colonies where they were reared. Movement to less productive habitat to avoid predation has been shown in a number of marine vertebrates (see above); in a natural experimental approach, a similar response has been observed among mesopredators with the reintroduction of apex predators (wolves, eagles, and falcons) to terrestrial ecosystems (Lank et al. 2003; Ripple and Beschta 2004; Ydenberg et al. 2004; Prugh et al. 2009). In the latter cases, herbivores and mesopredators vacate the productive riverine or other habitat where vision is obscured by dense vegetation, or change their migration routes in a major way, opting for habitat where predators are much fewer and in clear view (reviewed in Ydenberg et al. 2004; Wirsing and Ripple 2010).

We hypothesize that the high mortality suffered by fledgling emperor penguins while still in productive waters is due to predation, and further that killer whales could well be involved. Leopard seals tend to remain associated with sea ice, which the emperor penguins leave behind. Killer whales on the other hand are present in these shelfbreak waters and, in the case of ecotype-B, are known to visit locations of emperor penguin colonies (e.g., Andrews et al. 2008). When the majority of killer whales depart, high-latitude waters remains to be determined, but eventually they do, in part, perhaps for their own calving (R. L. Pitman personal communication). Killer whale presence is now known to affect the migratory movements of cetaceans (Morrell 2011).

Final thoughts

We realize that we have offered a view contrary to the resource-structuring interpretation of ecosystem organization that currently pervades the marine scientific community (see review in Baum and Worm 2009; Terbrough and Estes 2010), especially in the Antarctic (Ainley et al. 2007). Pursuing the hypotheses we have posed will require, in accord with the studies reviewed above concerning predation risk—foraging benefit: (a) information on the penguins' prey availability, and (b) more quantified information on the behavior of both meso- and apex predators occurring in high density in Antarctic shelfbreak waters, especially killer whales, during the January–February period when recently fledged and weaned, and naïve, penguins and seals are abundant there thus to attract predators and increase predation susceptibility (e.g., Lauriano et al. 2007; Andrews et al. 2008; Visser et al. 2008; Pitman and Durban 2010). Further observation is needed as well on the direct interaction between emperor penguins and apex predators (Ainley et al. 2010b). As noted by Pitman and Durban (2010), the fact that killer whales apparently do not eat the hard parts of penguins has added further difficulty to quantifying predation on penguins other than by direct observation.

In recent years, it has become increasingly more accepted among marine ecologists that apex predators, including killer whales by direct and indirect means, are important in structuring foodwebs (Morrell 2011). In the case we have made for penguins, this involves the issue of where penguins will concentrate their foraging. Further, we have hypothesized that killer whale predation may be involved in the population regulation of emperor penguins (Ainley et al. 2010b), which also affects how many foragers are present in a given locality. However, our connections between prey and predators are constrained by lack of direct predation observations, which as noted are otherwise rare. In that regard, we wonder about the recent mysterious disappearance of a small colony of emperor penguins at Dion Islands (150 pairs), when the sea ice became much more open in that area owing to the effects of global climate change (Trathan et al. 2011). Recession in sea ice, in this case short term, was also involved with short-term increased mortality of emperor penguins at another colony, Pt Géologie (Ainley et al. 2010b). Dion Island is near to where Pitman and Durban (2010) for the first time away from sub-Antarctic islands reported eye witness accounts of killer whales taking a significant number of Antarctic penguins, though not emperors which would not have been present at the time of season of their study. While the penguins they saw eaten were of a smaller species, their observations were near to Dion Island, and recent modeling by Reisinger et al. (2011) would indicate that the much larger emperor penguin would be of much greater interest to these predators. It would not take much predation to deplete such a small colony. In summary, the behavior of emperor and Adélie penguins that we have detailed indicates to us that killer whale and leopard seal predation is significant enough that their penguin prey have accordingly altered their behavior to avoid being eaten in ways similar to other air-breathing (prey) species (see summary also in Wirsing et al. 2008).

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