# From trips to bouts to dives: temporal patterns in the diving behaviour of chick-rearing Adélie penguins, East Antarctica

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ABSTRACT: Breeding Adélie penguins forage at sea and return to land to provision their chicks, adjusting their foraging behaviour in response to environmental fluctuations over time. At Béchervaise Island, a nesting site in an East Antarctic population, Adélie penguin diving behaviour remains undocumented. This represents a key area of uncertainty in efforts to understand and predict foraging success at this colony. We compiled a multi-year telemetry dataset from time–depth recorders deployed from 1992 to 2004 on 64 birds at Béchervaise Island. We examined diving activity at multiple scales, ranging from foraging trips (n = 125) to dive bouts (n = 3461) to individual dives (n = 84 521), and then characterised the stage- and sex-specific variation in diving behaviour of chick-rearing Adélie penguins using linear mixed effect models. Total foraging trip effort (trip duration, number of dives, vertical distance travelled and number of wiggles [a proxy for prey ingestion]) substantially increased as the chick-rearing period progressed (guard through crèche), consistent with increasing chick provisioning and self-maintenance requirements over time. Foraging activity was predominantly structured in periods of sustained diving bouts, indicating sustained foraging effort over the course of the foraging trip. Diving behaviour (dive-level depth, duration, bottom time and attempts of catch per unit effort) varied in relation to sex and chick-rearing stage. Dives were performed more frequently during high and low levels of solar light, which is likely linked to visual predation strategies or prey activity. Our findings advance our understanding of this population's foraging behaviour, which is ultimately required to underpin the conservation and management of this breeding colony.

KEY WORDS: Foraging behaviour · *Pygoscelis adeliae* · Diving · Chick provisioning · Guard · Crèche · East Antarctic

## 1. INTRODUCTION

Adélie penguins *Pygoscelis adeliae* have a circumpolar distribution and are among the most extensively studied Southern Ocean predators (Ainley 2002, Ancel et al. 2013). These seabirds have a strong association with the sea-ice environment (Emmerson & Southwell 2008, Lescroël et al. 2014, Le Guen et al. 2018) and are also important consumers of krill (Ainley 2002, Nicol et al. 2008, Tierney et al. 2009). As a func-

tion of these ecological attributes, Adélie penguins are highly sensitive to ecosystem change (Ropert-Coudert et al. 2018). Fluctuations in their population dynamics can be an indication of broader ecosystem structure and functioning (Constable et al. 2000, Ainley 2002). As indicators of ecosystem status, Adélie penguins are among the key study species under the Commission for the Conservation of Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP) (Agnew 1997, Ainley 2002).

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Individual-level foraging success has significant implications for the fitness, survival and reproductive performance of Adélie penguins. Natural selection operates at the level of the individual, and therefore, an individual's capacity to acquire resources and maximise energy can have consequences for population trends and characteristics (Sutherland 1996, Kokko & López-Sepulcre 2006). Foraging success has been identified as a key determinant of Adélie penguin survival and reproductive success (Ballard et al. 2010, Lescroël et al. 2010), with multiple episodes of total breeding failure linked to poor foraging conditions (Emmerson & Southwell 2008, Ropert-Coudert et al. 2015, 2018). Determining the biological and physical factors which drive spatial and temporal changes in foraging success can help develop better predictive capacity, for example the likelihood of ecosystem-level impacts and responses under future krill harvesting and climate scenarios (Forcada & Trathan 2009, Ainley et al. 2010, Lynch et al. 2012).

During the austral summer breeding season, Adélie penguins are central-place foragers, leaving the colony to locate and capture prey in a 3-dimensional, heterogeneous marine environment and returning to the colony to assume incubation duties or feed their chicks. Foraging effort comprises movement in both the horizontal and vertical dimensions (Ainley 2002). Knowledge gaps in relation to these vertical and horizontal foraging components, and how they relate to the prey field and sea-ice conditions, represent key areas of uncertainty in efforts to understand and predict foraging success (Emmerson et al. 2015, Takahashi et al. 2018, Saenz et al. 2020).

For Adélie penguins, diving is a fundamental component of foraging and acquiring energy. Foraging effort is amplified during the breeding season, when breeding pairs must acquire energy for themselves and their chicks (Ainley 2002, Thiebot et al. 2019). During this period, diving movements are constrained by a variety of intrinsic and extrinsic factors. Intrinsic constraints include basic self-maintenance necessities, physiological condition and requirements to return to the colony to provision chicks. Extrinsic constraints include proximity of foraging grounds to nesting sites, physical barriers posed by sea ice and levels of biological productivity influencing prey abundance (Lescroël et al. 2010, Emmerson et al. 2015, Saenz et al. 2020). Adélie penguins change their foraging behaviour during the breeding cycle in response to environmental variability, fluctuations in the prey field, parental body condition and chick provisioning requirements over time (Clarke et al. 2006, Tierney et al. 2009, Ballard et al. 2010). Determining

how these intrinsic and extrinsic factors shape diving behaviours and success can yield insight into how Adélie penguin populations may respond to seasonal and inter-annual changes in prey availability, and to environmental change more broadly (Emmerson et al. 2015, Le Guen et al. 2018, Takahashi et al. 2018).

Diving activity of chick-rearing Adélie penguins has been reported in East Antarctica at Lützow-Holm Bay (Kato et al. 2003, Watanuki et al. 2010), Prydz Bay (Whitehead 1989, Watanuki et al. 1997) and Dumont d'Urville (Rodary et al. 2000, Ropert-Coudert et al. 2002, Le Guen et al. 2018), as well as colonies in the Ross Sea (Lescroël et al. 2010, 2020, Nesti et al. 2010, Lyver et al. 2011, Ainley et al. 2015, Ford et al. 2015) and the Antarctica Peninsula (Chappell et al. 1993). However, many studies have been restricted by sampling over limited temporal scales, with few comparing diving activity between the 2 chick-rearing stages, i.e. guard and crèche (Rodary et al. 2000, Lescroël et al. 2010, Nesti et al. 2010, Lyver et al. 2011). Furthermore, substantial inter-colony differences are evident in Adélie penguin foraging behaviour, driven by regional variation in physical and environmental features, prey distribution and intra- and inter-specific competition (Lescroël et al. 2010, Watanuki et al. 2010, Ford et al. 2015). To better understand how diving effort changes throughout the chick-rearing season, there is a need to examine colony-specific diving activity across a range of temporal scales.

In this study, we examined the historical dive data available for the Béchervaise Island Adélie penguin colony to determine how diving behaviour varies between males and females through the chick-rearing period. Compiling an extensive multi-year telemetry dataset from bird-attached time–depth recorders (TDRs), we analysed a suite of diving parameters calculated during the guard and crèche stages. Temporal patterns and sex-specific variation in diving behaviour were characterised at multiple scales, ranging from foraging trips to diving bouts to individual dives. In quantifying vertical movements across these 3 scales, we expected (1) total and per unit time foraging effort would increase from guard to crèche, (2) males and females would exhibit markedly different foraging behaviour between chick-rearing stages, and (3) diurnal patterns in foraging behaviour would be evident, assuming that solar light influences visual predation strategies and prey vertical migrations. Our findings are discussed within the context of life history constraints and intraspecific diet variability, and the future outlook towards integrating diving behaviour with spatial movement and environmental informa-

tion to assess spatiotemporal patterns of forage resources used by this colony.

## 2. MATERIALS AND METHODS

### 2.1. Instrument deployment and processing of dive data

Adélie penguins have been a focus of long-term monitoring at Béchervaise Island (67° 35′ S, 67° 49′ E), a designated CEMP site, since 1990. Béchervaise Island is a nesting site which is part of an East Antarctic colony, with over 2000 breeding pairs (Kerry et al. 2000). TDRs were deployed over the breeding seasons between 1992/1993 and 2003/2004 and

covered both stages of the chick-rearing period: guard (late December to mid- to late January) and crèche (mid-January to early to mid-February) (Ainley 2002). Here, we collated dive data over the course of 10 breeding seasons (excluding the 1997–1998 and 1999–2000 seasons, for which data were not retrieved or useable). The dive records in this study represent 64 penguins over 125 different foraging trips (Fig. 1; Table S1 in the Supplement at www.int-res.com/articles/suppl/m654p177_supp.pdf).

Breeding individuals were captured at nests, and their breeding status and weight were determined. Sex was determined by cloacal examination (Sladen 1978). TDRs were glued to feathers on the lower back using rapid-hardening epoxy glue (Loctite 401™) and
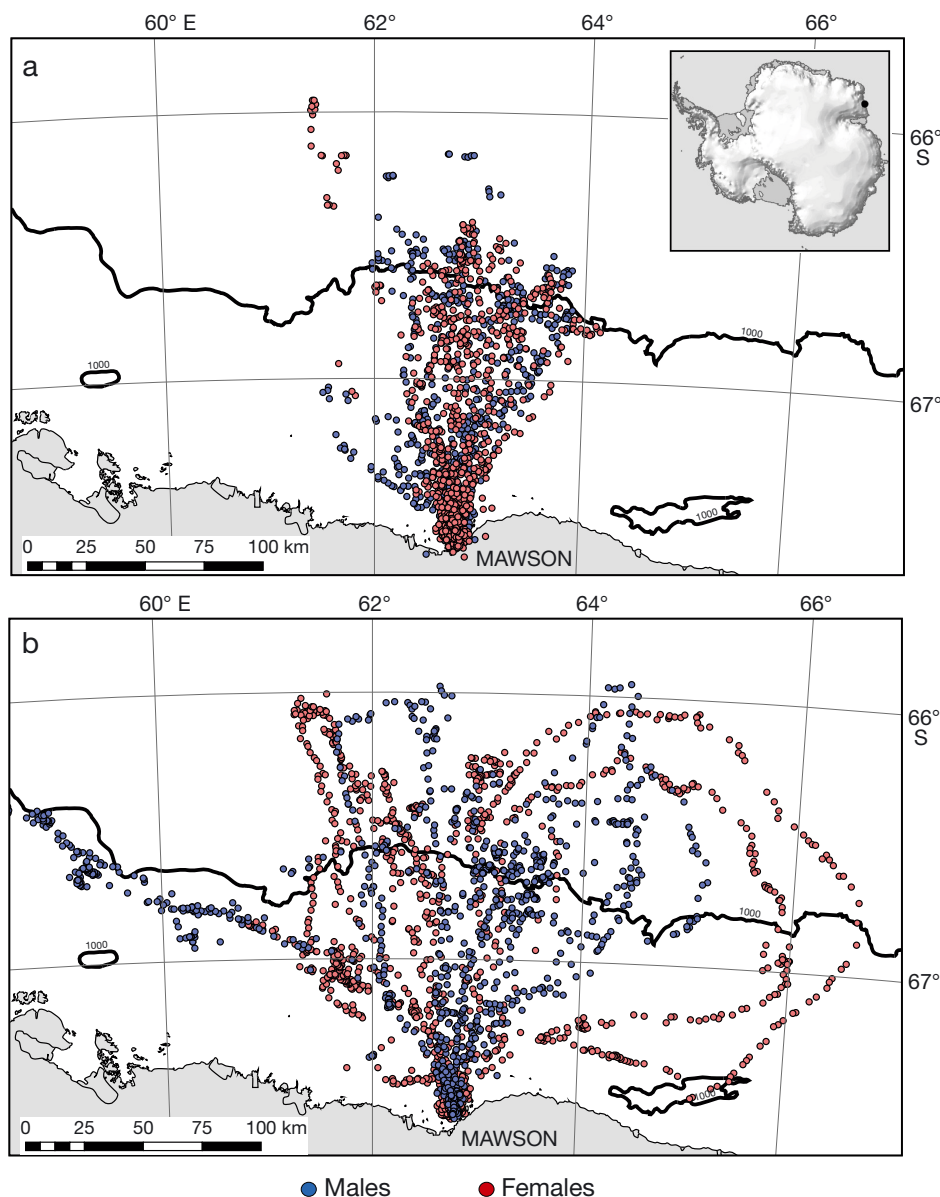


Fig. 1. Satellite tracking locations of Adélie penguins at Béchervaise Island, East Antarctica. See Clarke et al. (2006) for a description of instrument deployment and location data processing. Distribution of individuals (blue: males; red: females) examined in this study are displayed during (a) guard and (b) crèche. Data span the chick-rearing seasons between 1991/1992 and 2003/2004. Major bathymetric features, such as the shelf break, are indicated by black lines. Major land and ice features are shown in grey. Inset in panel (a) shows the study region (black circle) in East Antarctica

secured with cable ties threaded under the feathers and around the device. Individual birds carried TDRs for 1 to 6 consecutive foraging trips during each deployment. Removal of TDR devices was achieved by cutting cable ties and breaking the underlying layer of glue. The dive records were obtained using 2 different TDR models. Wildlife Computers Mk5 TDRs were used for 4 breeding seasons between 1992 and 1999. These weighed 50 g, measured 65 × 35 × 15 mm and recorded depth in 5, 2 or 1 s increments with a ±1 m resolution. From the year 2000 onwards, Mk7 TDRs were deployed. These devices weighed 30 g, measured 98.5 × 20 × 10 mm and recorded depth every 1 s with a ±0.5 m resolution. Foraging trip durations were recorded to the nearest second as individually tagged penguins crossed a custom built automated penguin monitoring system (APMS) on their way in and out of the colony (Kerry et al. 1993). Trip duration records from APMS data were cross-referenced with nest censuses, as described by Clarke et al. (2002). TDRs were fitted to penguins already carrying an implanted, individually unique, electronic identification tag (Clarke & Kerry 1994).

Archived dive data were downloaded using Wildlife Computers software packages. A zero-offset correction was applied to depth readings to account for shifts in the TDR pressure transducer. Dives <3 m were excluded from analyses, as wave action and surface noise prevent accurate discrimination of shallow dives (Beck et al. 2000, Luque et al. 2008). All subsequent analyses were performed with custom code using R version 3.5.1 (R Core Team 2018).

## 2.2. Foraging trip, bout and dive analyses

A total of 106 017 dives were recorded over the 10 yr period. Each dive was categorised into descent, bottom and ascent phases based on inflexion points. The bottom phase was determined by abrupt changes in the descent and ascent slopes. The start of the bottom phase was assigned to the first point within 50% of the maximum dive depth where the rate of change in depth during descent decreased by 50%, with the start of the ascent phase determined in reverse. The maximum depth (m), duration (s) and surface interval (s) of each dive was extracted. The number of wiggles for each dive was also calculated. This metric represents the number of deviations in the dive profile >2 m in depth and has been associated with prey ingestion for penguins (Bost et al. 2007, Hanuise et al. 2010, Watanabe & Takahashi 2013). To examine foraging behaviour, we restricted our analyses to for-

aging dives. Foraging and non-foraging (travelling and searching) dives have been identified for penguins using a variety of different criteria (Tremblay & Cherel 2003, Green et al. 2005). We considered foraging behaviour to be indicated by dives >15 m deep, or any dive <15 m which also displayed wiggle activity, criteria analogous with other Adélie penguin diving studies (Chappell et al. 1993, Rodary et al. 2000). To evaluate foraging effort and behaviour, we examined movement at different scales ranging from foraging trips to diving bouts to individual dives. Across all scales, diving activity was examined in relation to sex and stage. Differences in TDR sampling rates (5, 2 and 1 s) between deployment seasons may introduce a bias in our analyses of diving parameters. Dive-level wiggle metrics were identified as being potentially sensitive to different sampling rates, since wiggles occur on fine scales (of seconds and metres); therefore, analyses of these metrics were restricted to include only individuals fitted with TDRs recording at 1 s sampling intervals (n = 78).

### 2.2.1. Trip level

Dive activity was examined at the scale of the foraging trip to identify sex- and stage-related trends in foraging effort through the chick-rearing period. Trip-level metrics, such as foraging trip duration, correlate positively with energy expenditure in Adélie penguins (Ballance et al. 2009). For each individual, the duration of foraging trips and number of foraging dives performed in a foraging trip was examined. We also summed the depth, duration, number of wiggles and bottom phase duration of each dive performed during a foraging trip. Based on a literature review, we calculated a variety of derived indices at the scale of the foraging trip to minimise potential biases and correlations (Table 1).

### 2.2.2. Bout level

Investigating diving activity at the level of dive bouts is expected to provide information about prey availability and aggregations (Chappell et al. 1993, Le Guen et al. 2018). Diving bouts are defined as periods of high-intensity foraging activity consisting of multiple dives in quick succession (Luque & Guinet 2007). Sequential foraging dives were clustered into diving bouts using a maximum likelihood estimation method based on the absolute differ-

Table 1. Derived diving metrics used to examine Adélie penguin trip-, bout- and dive-level diving behaviour. Each metric was calculated across all dives per trip per individual

| Derived diving metrics | Calculation | Explanation | Examples of usage |
|---|---|---|---|
| **Trip-level derived metrics calculated from dive information** | | | |
| Dive frequency | $\dfrac{\text{Number of dives per foraging trip}}{\text{Foraging trip duration}}$ | Number of dives per unit of time (here, dives per hour) | Staniland et al. (2010), Antarctic fur seals |
| Vertical dive rate | $\dfrac{\text{Vertical distance travelled}}{\text{Foraging trip duration}}$ | Total sum of the maximum dive depth of each individual dive divided by the total trip duration (here, m per hour) | Zimmer et al. (2008b), emperor penguins; Pütz et al. (2006), southern rockhopper penguins |
| Proportion of bottom time | $\dfrac{\text{Total time spent in bottom duration}}{\text{Total time submerged}}$ | Proportion of time spent in the bottom phase (expected foraging) during dives | Halsey et al. (2010), king penguins |
| Attempts of catch per unit effort ($ACPUE_t$) | $\dfrac{\text{Total number of wiggles}}{\text{Total time in bottom duration}}$ | Total number of prey capture attempts (with or without success) relative to the total time spent in the bottom phase per trip | Zimmer et al. (2010), emperor penguins, Le Guen et al. (2018), Adélie penguins |
| **Bout-level derived metrics calculated from dive information** | | | |
| Proportion of dives in bouts | $\dfrac{\text{Number of bout dives per foraging trip}}{\text{Total number of dives per foraging trip}}$ | Proportion of the total dive number allocated as bout diving | Lea et al. (2002), Luque et al. (2008), Antarctic fur seals |
| **Dive-level derived metrics calculated from dive information** | | | |
| Attempts of catch per unit effort ($ACPUE_d$) | $\dfrac{\text{Number of wiggles}}{\text{Bottom duration}}$ | Number of prey capture attempts (with or without success) relative to individual bottom duration | Refer to trip-level ACPUE above |

ences in diving intervals (Luque & Guinet 2007), which was executed using the 'diveMove' package in R (Luque 2007). Before running the bout analysis, lengthy post-dive intervals greater than 1200 s were removed. The bout-ending criterion (BEC) was first determined for males and females separately, and was estimated as 295 and 282 s, respectively. Given the minor difference (<15 s) in sex-specific BEC values, data were pooled and a single BEC value was generated for all individuals, which was 288 s. Post-dive surface intervals >288 s indicated the occurrence of a new foraging bout. Bouts were required to comprise a minimum of 3 dives. Once the minimum bout criteria were satisfied, we examined the number of bouts in a foraging trip and the number of dives comprising a single bout. With these bout metrics, we also calculated the rate of bout activity in a foraging trip (Table 1).

### 2.2.3. Dive level

The final level of analysis examined diving activity considering all individual foraging dives, to provide insight into how female and male Adélie penguins modify the structure of their dive cycle through the chick-rearing season. Here, we evaluated basic diving parameters: dive depth (m), dive duration (s), bottom duration (s) and 2 wiggle metrics (excluding 5 and 2 s TDR sampling rates), i.e. number of wiggles per dive and attempts of catch per unit effort ($ACPUE_d$) (see definitions in Table 1). To specifically investigate any diurnal patterns in diving activity, we examined these diving parameters in relation to solar position. Depending on the time at which it occurred, each dive was assigned a solar position value using the 'solarpos' and 'solarnoon' functions in the R package 'maptools' (Bivand & Lewin-Koh 2016). Given that chick-rearing

Adélie penguins forage in close proximity (60 and 125 km in guard and crèche, respectively) to their breeding sites (Clarke et al. 2006), each dive time-stamp was assigned a solar position value based on the sun position at Béchervaise Island. Dives which were assigned solar position values below −12° equate to night-time, above 12° to daytime and between −12° and 12° to dawn/dusk depending on whether the dive occurred before or after solar noon.

## 2.3. Statistical analysis

Linear mixed effects models (LMMs) were fitted separately for trip-, bout- and dive-level foraging analyses ('lme' function, 'nlme' package; Pinheiro et al. 2018). Each LMM was fit including sex, stage and a sex×stage interaction term as fixed effects. The random effects structure was specified as individual penguin nested within year (i.e. Year/Bird) to allow year-to-year level variation and variation amongst individuals to be directly accounted for. We further configured the fixed effects structure of dive-level LMMs to account for the behavioural dependence of dive duration on depth, bottom duration on both dive depth and duration, $ACPUE_d$ on duration and wiggle activity on bottom duration. To examine diurnal patterns in diving behaviour, dive-level LMMs also included solar position as a fixed effect. Models were configured with and without a quadratic term, and model comparisons were performed using Akaike's information criterion (AIC). All dive-level LMMs were fit with a temporal autocorrelation term (cor-CAR1) to account for serial non-independence in the timeseries data. For each LMM, diving metrics were either log-transformed, or else logit transformed for proportion data. Model terms were considered significant at $p < 0.05$. Normality requirements were examined using QQ plots.

## 3. RESULTS

Across 64 individual birds, TDRs provided information on 125 foraging trips, 3461 dive bouts and 84 521 foraging dives. Aggregating the data from all years together, observations of diving activity spanned from 29 December to 4 February. Over the duration of the chick-rearing season, we found that the number of dives and individual birds recorded in the water at any given time was greatest towards the end of guard and beginning of crèche (i.e. mid-January) (Fig. S1).

### 3.1. Trip level

Clear differences were evident in trip-level metrics of foraging effort calculated for guard and crèche. Mean duration of foraging trips was 32 and 42 h in guard, and 96 and 66 h in crèche, for males and females, respectively (see Table 2 for means and 95% CI). Dive frequency, trip-level attempts of catch per unit effort ($ACPUE_t$) and the proportion of bottom time did not vary in relation to sex or stage. Vertical dive rate varied only in relation to sex, with males covering more vertical distance per hour of diving than females. A sex-stage interaction was evident in foraging trip duration, which increased as the chick-rearing period progressed from guard through to crèche; this pattern was significantly more pronounced for males. The same pattern was observed

Table 2. Trip-level summaries of Adélie penguins foraging at Béchervaise Island (n = 64 birds, n = 125 trips). All values represent the means of males and females over the guard and crèche stages of chick-rearing, compiled across the 10 seasons. Proportion of bottom time, which was logit transformed in linear mixed effects models, is presented as an arithmetic mean ± SD. All other metrics are presented as geometric means (95% confidence interval). See Section 2 for details of data transformations. Number of trips for each sex-stage combination is provided. Derived diving parameters defined as per Table 1

| Diving parameter | Guard (n = 90 trips) | | Crèche (n = 35 trips) | |
|---|---|---|---|---|
| | Female (n = 40 trips) | Male (n = 50 trips) | Female (n = 15 trips) | Male (n = 20 trips) |
| Foraging trip duration (h) | 42 (9–193) | 33 (7–146) | 66 (10–425) | 96 (26–354) |
| Dives per foraging trip | 576 (85–3907) | 311(45–2177) | 1023 (172–6067) | 1578 (479–5192) |
| Vertical distance travelled (km) | 13 (2–71) | 10 (2–59) | 23 (5–101) | 37 (13–100) |
| Number of wiggles | 2077 (260–16575) | 1443 (132–15698) | 3809 (223–65174) | 6322 (811–49295) |
| Vertical dive rate (m h$^{-1}$) | 312 (122–798) | 410 (138–1218) | 354 (133–940) | 382 (187–781) |
| Proportion of bottom time | 0.49 ± 0.10 | 0.48 ± 0.11 | 0.46 ± 0.09 | 0.50 ± 0.08 |
| $ACPUE_t$ % | 15 (6–36) | 14 (6–35) | 16 (8–31) | 17 (11–28) |
| Foraging dive frequency (dives h$^{-1}$) | 15 (8–31) | 15 (8–29) | 16 (9–26) | 16 (9–30) |

for the total number of dives, total vertical distance travelled and total number of wiggles (Fig. 2; see Table S2 for full model results).

## 3.2. Bout level

A total of 3461 diving bouts were recorded over 125 foraging trips. Adélie penguin diving activity at this colony showed a high degree of temporal organisation, with foraging dives predominantly (70 % of dives) structured in periods of sustained diving bouts. On average, bouts consisted of 12–14 dives (see Table 3 for means and 95 % CI). The model results for the total number of dive bouts were consistent with the changes reported above for foraging trip duration, i.e. showing a significant sex×stage interaction, with an increase from guard
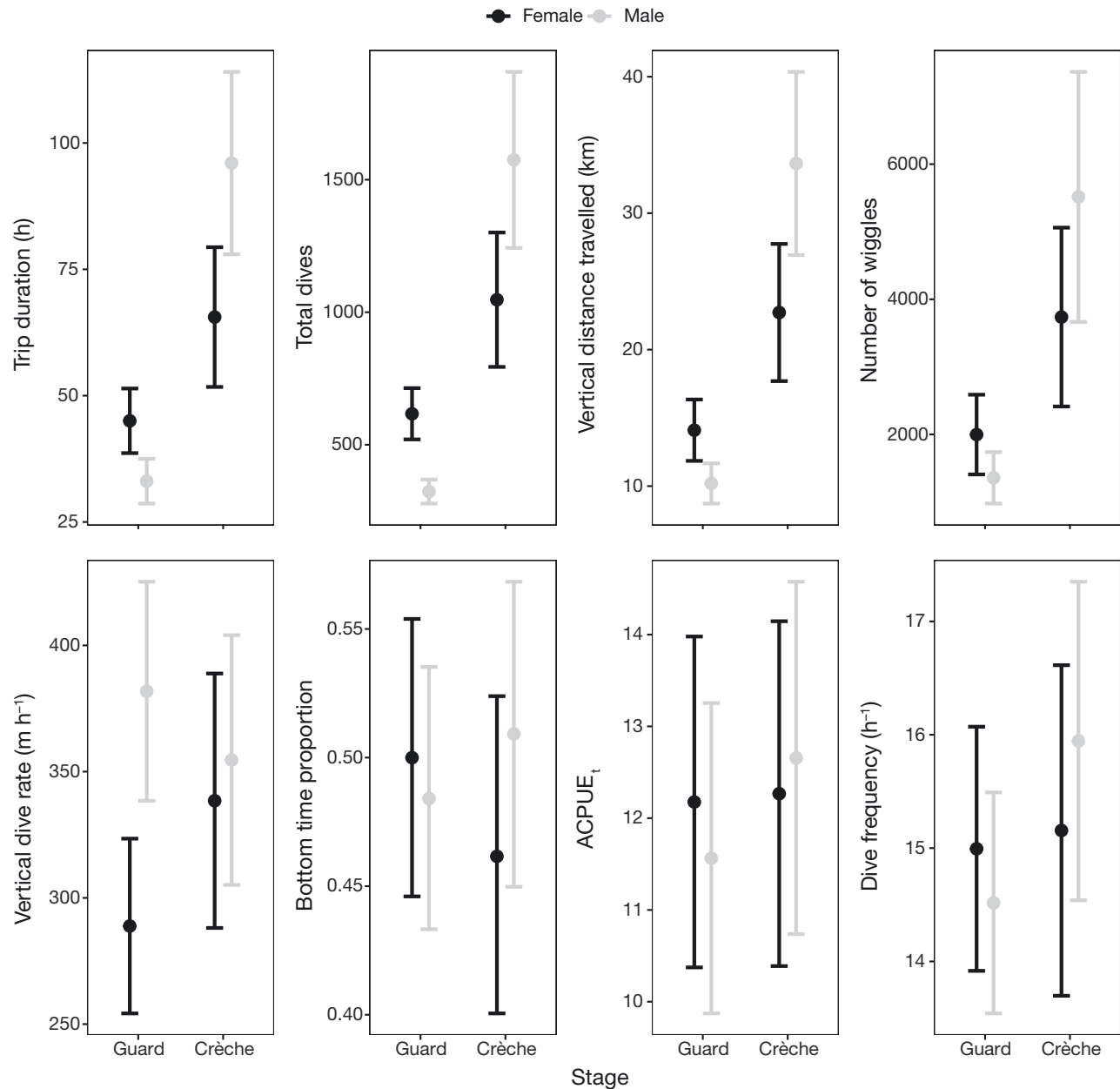


Fig. 2. Model results for trip-level diving parameters in relation to chick-rearing stage (guard and crèche) for Adélie penguin females (black) and males (grey). Results are presented as the back-transformed estimated means (95 % confidence intervals) from fitted linear mixed effects models, plotted using the 'effects' package in R (Fox 2003). See Section 2 for details of data transformations. See Table 1 for definitions and units of derived diving parameters and Table S2 for full model results

Table 3. Bout-level summaries of Adélie penguins foraging at Béchervaise Island (n = 64 birds, n = 125 trips, n = 3461 bouts). Proportion of dives in bouts, which was logit transformed in linear mixed effects models, is presented as an arithmetic mean ± SD. All other metrics are presented as geometric means (95% confidence interval). See Section 2 for details of data transformations. Results presented as in Table 2

| Diving parameter | Guard (n = 90 trips) | | Crèche (n = 35 trips) | |
|---|---|---|---|---|
| | Female (n = 40 trips) | Male (n = 50 trips) | Female (n = 15 trips) | Male (n = 20 trips) |
| Total number of bouts | 17 (3–99) | 11 (2–69) | 30 (4–228) | 44 (12–158) |
| Dives per bout | 12 (2–90) | 12 (1–92) | 14 (2–97) | 14 (2–113) |
| Proportion of dives in bouts | 0.68 ± 0.16 | 0.75 ± 0.13 | 0.75 ± 0.14 | 0.73 ± 0.11 |

to crèche that was more pronounced for males (Fig. 3; see Table S3 for full model results). The number of dives within a bout did not vary in relation to sex or stage. The proportion of dives occurring in bouts showed a complex sex/stage influence, with the interaction being the only significant term; this indicates opposing effects, where the predicted change from guard to crèche was positive for females and negative for males (Fig. 3; see Table S3 for full model results).
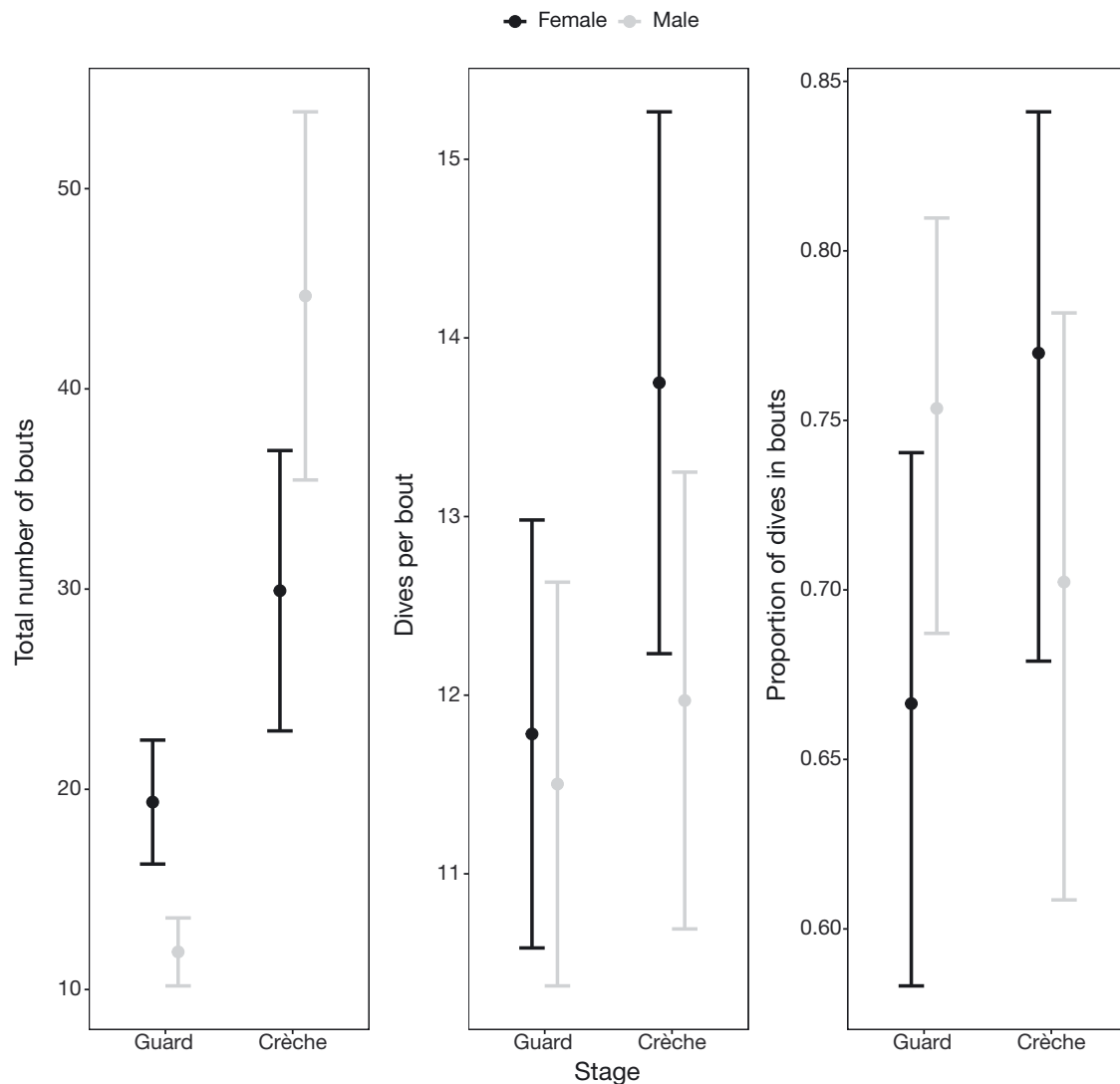


Fig. 3. Model results for bout-level diving parameters in relation to chick-rearing stage (guard and crèche) for Adélie penguin females (black) and males (grey). Results are presented as back-transformed estimated means (95% confidence intervals) from fitted linear mixed effects models, as in Fig. 2. See Table 1 for definitions and units of derived diving parameters and Table S3 for full model results

### 3.3. Dive level

Across the 84 521 recorded foraging dives, the maximum dive depths recorded by TDRs were 115 and 120 m for females and males, respectively. Forage dives occurred with the highest frequency at shallow depths of 5–10 m, becoming less frequent with increasing depth (Fig. S2). The mean dive depths were near 20 m, and dives typically lasted around 1 min each (see Table 4 for means and 95% CI). Most dive-level metrics varied in relation to sex and stage. Model results showed that dive duration was positively correlated with dive depth, while bottom duration was negatively correlated with dive depth but positively correlated with dive duration. However, these expected behavioural trends varied between sexes. For males, crèche dives were shallower with a shorter duration, and bottom duration was also marginally reduced. In contrast, females dived to similar depths throughout the chick-rearing period, but dives during crèche had a longer bottom phase and duration. The number of wiggles per dive was positively correlated with dive bottom duration, and $ACPUE_d$ was negatively correlated with duration. During the crèche period, dives consisted of fewer wiggles. While $ACPUE_d$ decreased for both sexes, this pattern was more pronounced for females (Fig. 4; see Table S4 for full model results).

Diurnal influences on diving activity and behaviour were evident for Adélie penguins at this Béchervaise Island colony. The dive-level LMMs revealed relatively complex associations with solar position (Fig. 4; see Table S4 for full model results), with dive depths being deeper at both higher and lower solar light levels (significant positive quadratic relationship, see also Fig. 5a), while dive duration decreased with increasing levels of light. Consequently, bottom duration showed the opposite relationship to depth (i.e. significant negative quadratic relationship to solar position), indicating that longer bottom times occurred at intermediate light levels. Wiggles and $ACPUE_d$ also increased with increasing levels of light. Over the observed chick-rearing period (29 December to 4 February), solar position ranged between −6.24° and 45.71°, never dipping below nautical twilight (i.e. 12° below the horizon). Therefore, penguins did not perform any 'night diving'. While diving activity was recorded throughout the available solar light levels, the frequency of foraging dives was quadratically distributed. Dives were most frequently performed during high levels of light near midday and low levels of light around dawn. Across all dives recorded, 37.5% took place during the dawn period (<12° above the horizon), 62.0% during the day and only 0.5% at dusk (Fig. 5b).

## 4. DISCUSSION

Our study provides an assessment of diving activity across multiple scales. Importantly, the trip-, bout- and dive-level modelling approaches outlined here may be applied to vertical movement analyses for other air-breathing marine predator taxa. Our findings provide valuable insight into the underwater foraging behaviour of Adélie penguins and are generally consistent with the sex-specific foraging strategies identified throughout the chick-rearing period at Béchervaise Island (Clarke et al. 1998, 2002, Tierney et al. 2009). Integrating our scaled diving metrics with spatial movement and dynamic environmental information will support the assessment of key foraging areas and spatiotemporal patterns of forage resources used by this breeding colony.

### 4.1. Diving characteristics and structure

Determining the basic characteristics and structure of Adélie penguin diving behaviour is important in understanding fine-scale foraging activity. At Béchervaise Island, penguins performed dives at a wide range of depths. However, most foraging dives were relatively shallow, occurring within the first 10 m of the water column. These diving patterns are consistent with observations from other locations in East Antarctica, such as Lützow-Holm Bay and Dumont

Table 4. Dive-level summaries of Adélie penguins foraging at Béchervaise Island (n = 64 birds, n = 125 trips). All metrics are presented as geometric means (95% confidence interval). See Section 2 for details of data transformations. Results presented as in Table 2

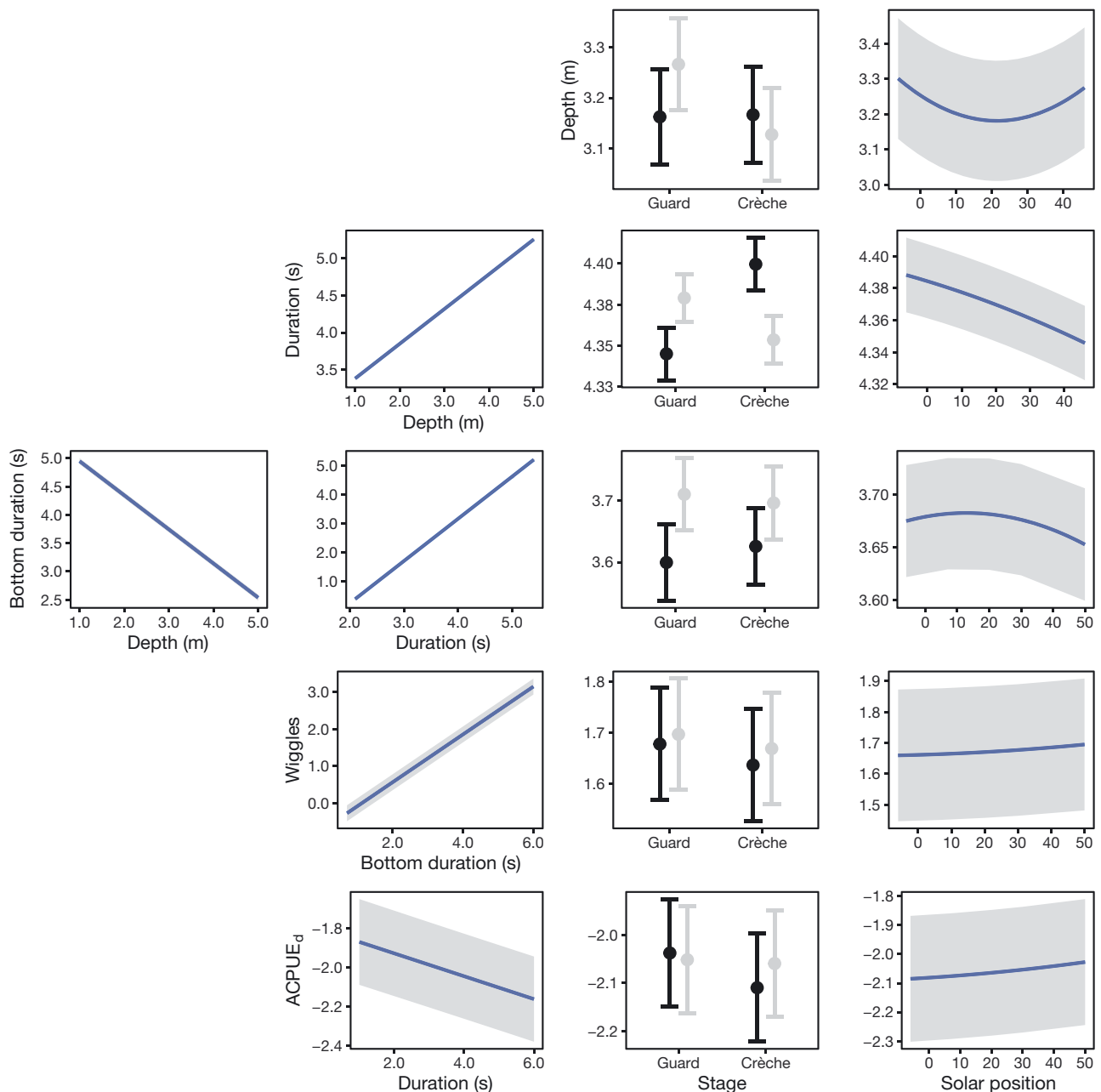| Diving parameter | — Guard (n = 90 trips) — | | — Crèche (n = 35 trips) — | |
| | Female (n = 40 trips) | Male (n = 50 trips) | Female (n = 15 trips) | Male (n = 20 trips) |
| --- | --- | --- | --- | --- |
| Dive depth (m) | 23 (5–114) | 25 (5–135) | 20 (4–105) | 21 (4–109) |
| Dive duration (s) | 78 (33–185) | 82 (34–205) | 76 (33–179) | 77 (32–189) |
| Bottom duration (s) | 37 (14–97) | 41 (16–104) | 39 (16–95) | 40 (17–97) |
| Number of wiggles per dive | 6 (2–20) | 7 (2–22) | 7 (2–22) | 7 (2–23) |
| $ACPUE_d$ per dive % | 15 (5–48) | 15 (5–48) | 16 (5–48) | 17 (5–50) |

Fig. 4. Results for Adélie penguin dive-level parameters modelled in relation to other dive parameters, chick-rearing stage (guard and crèche), sex (females: black; males: grey) and solar position (quadratic term). The solid blue lines represent the regression fit to observations, and the grey shaded area indicates the 95% confidence intervals (CIs). Tight CIs are not visible in panels displaying the relationship between diving parameters, with 2 exceptions (wiggles in relation to bottom duration and ACPUE$_d$ in relation to duration). All dive metric axes are natural log transformed and presented as in Fig. 2. See Table 1 for definitions and units of derived diving parameters and Table S4 for full model results

d'Urville (Ropert-Coudert et al. 2001, Kato et al. 2003, 2009) and likely reflect under-ice foraging tactics and the vertical distribution of dominant prey items, such as Antarctic krill *Euphausia superba* and fish (e.g. *Pagothenia borchgrevinki*), during the chick-rearing period (Brierley et al. 2002, Watanabe & Takahashi 2013).

Foraging dives were predominantly structured in periods of sustained diving bouts. This is also consistent with our understanding of Adélie penguin foraging activity derived from other colonies (Chappell et al. 1993, Ford et al. 2015, Le Guen et al. 2018). Krill and fish are both important components in the diet of chick-rearing Adélie penguins at Béchervaise Island
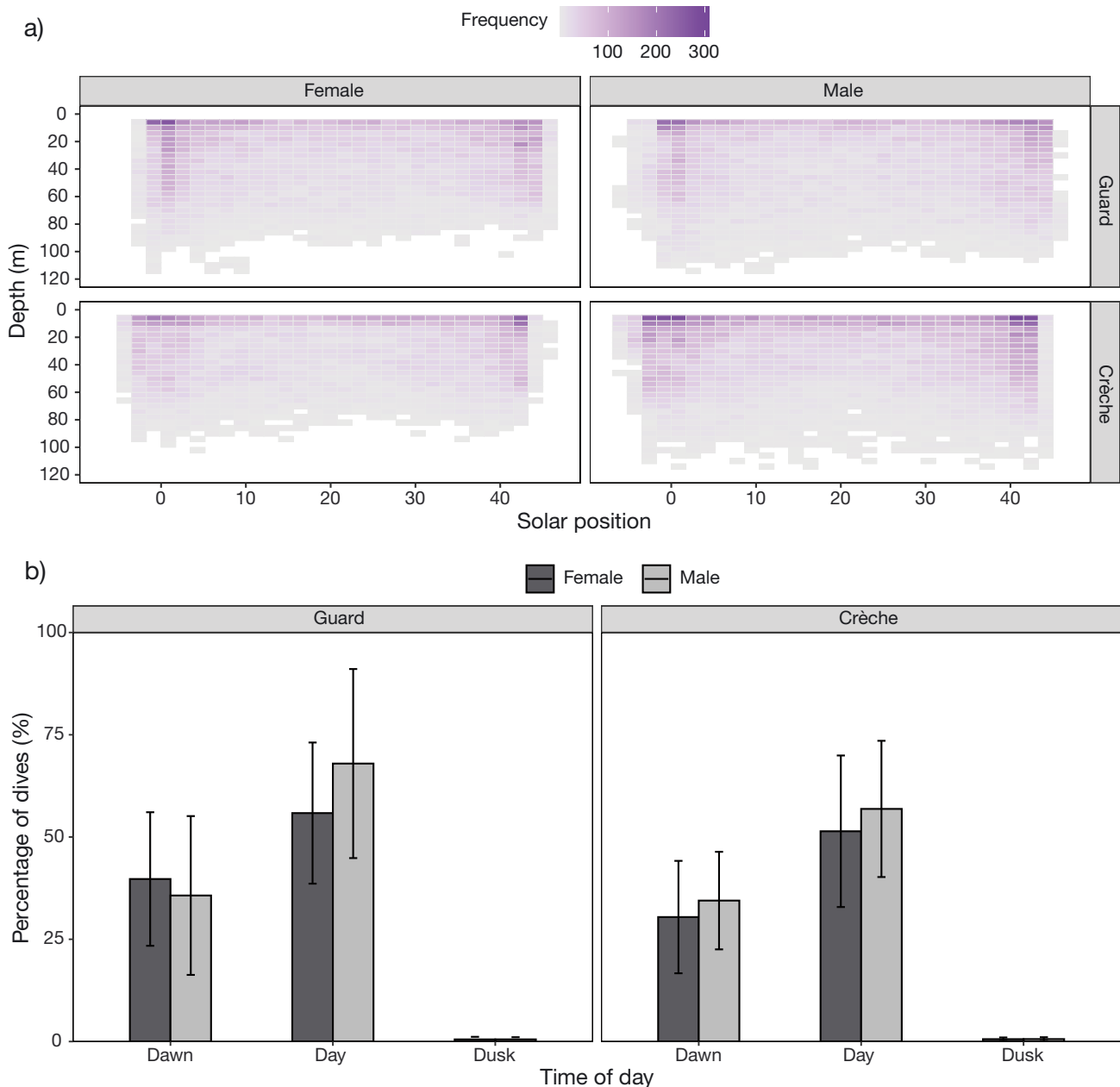
Fig. 5. Compiled time−depth recorder data showing the recorded observations of diurnal diving behaviour through time (total n = 64 birds, n = 84 521 foraging dives). Displayed is the (a) frequency of diving activity in relation to depth and solar position and (b) percentage diving activity at times designated as dawn, day and dusk (see Section 2 for details of diurnal categories). Plots are separated by sex and stage (guard, crèche)

(Clarke et al. 2002, Tierney et al. 2009). Krill are prey items which generally occur in aggregations or 'swarms' of varying scale (Nicol et al. 2008, Bestley et al. 2018). In East Antarctica, regional-scale acoustic surveys show high biomass density estimates concentrated particularly along the shelf-break (Jarvis et al. 2010). Furthermore, dominant fish prey items, such as *Pleuragramma antarcticum*, are also known to aggregate in loose shoals (Fuiman et al. 2002).

Assuming bout activity reflects prey patch foraging for marine predators (Chappell et al. 1993, Luque et al. 2008), our results suggest Adélie penguins at the Béchervaise Island colony tend to forage within prey aggregations or patches.

However, a high degree of bout activity need not exclusively correspond to a model of commuting to, and foraging within, prey patches in a heterogeneous prey field. Similar to Adélie penguins in the

Ross Sea (Ford et al. 2015), sustained bout activity for the Béchervaise Island population may reflect high prey availability relative to their rate of consumption. This could be driven by horizontal and vertical transport restoring prey abundance, or alternatively, penguins continuously and opportunistically foraging over the course of the foraging trip (Ford et al. 2015). Our findings of no sex- or stage-related difference in the number of dives comprising a bout supports this idea, suggesting that the temporal organisation of foraging dives within a foraging bout is limited by physiological constraints rather than by prey availability (Ford et al. 2015). Further information on penguin horizontal–vertical movement relationships, and how they relate to regional prey-field characteristics, is needed to validate these interpretations about diving activity for Adélie penguins at this colony.

Wiggles are commonly used as a metric of foraging behaviour for penguins and other diving marine predators to infer prey capture attempts (Roncon et al. 2018). For Adélie penguins at Béchervaise Island, an increased number of wiggles corresponded to increased time spent in the bottom phase of dives, indicating that most prey capture attempts likely occurred in the bottom phase (Bost et al. 2007). We also found that an increased amount of time spent in the bottom phase corresponded with a longer total dive duration. Conversely, increasing dive depth was associated with a reduced bottom time. These results may be a function of optimal foraging strategies in the context of breath-holding limitations (Chappell et al. 1993). Travelling to depths generally has a greater cost on energy and oxygen reserves, particularly for smaller divers, therefore reducing the proportion of dive time which can be dedicated to foraging. Hence, prey capture attempts can be maximised during shallow feeding opportunities. This has interesting implications when considering the role of sea-ice in aggregating shallow prey (Nicol 2006), and potentially creating a floor-like barrier or ceiling which can trap prey and essentially modify the typical shape of the dive structure, resulting in an inverted dive bottom in the upper 5–10 m. This warrants further exploration of Adélie penguin dive behaviour in relation to both sea ice and prey-field distribution and characteristics.

## 4.2.  Diurnal patterns in diving behaviour

As expected, the diving strategies of Adélie penguins at Béchervaise Island appear to be influenced by solar light. Although diving activity was recorded throughout the day, dives most frequently occurred during high levels of light (around midday) and low levels of light (at dawn). Hence, there may be optimal foraging times, influenced by diel vertically migrating prey and visual predation strategies. In an effort to avoid visual predators, krill migrate to the surface at night and return to depths through the day (Trathan & Hill 2016). The high proportion of dawn dives corresponds with the expected vertical migratory behaviour of *E. superba*, a dominant prey item. Lower light levels at dawn may represent a time where *E. superba* are still at the surface and remain available, while light levels are sufficient to facilitate visual prey detection and capture (Chappell et al. 1993, Zimmer et al. 2008a, Regular et al. 2010). Conversely, diving during high light levels may be a strategy to optimise visual predation efforts and hunting efficiency (Zimmer et al. 2008a, Ballard et al. 2019). As well as exhibiting diurnal patterns in foraging times, penguins at Béchervaise Island also modified their diving behaviour in accordance with solar light. Generally, at high and low levels of light, dives were deeper and correspondingly had reduced bottom time. However, dives performed at high light levels were of shorter duration with increased wiggle activity. These complex behavioural patterns suggest that Adélie penguin foraging strategies differ with solar light, which is likely related to prey dynamics during these times, such as type, availability and aggregation (Rodary et al. 2000). It is also possible that predator avoidance may play a role in the diurnal foraging activity of Adélie penguins (Ainley et al. 2005).

The few studies which have examined diurnal foraging activity of Adélie penguins have largely focussed on dive frequency, recording no circadian pattern (Watanuki et al. 1997, Kato et al. 2009), or pronounced activity at either high (Chappell et al. 1993, Kato et al. 2009) or low light levels (Rodary et al. 2000, Takahashi et al. 2018). Furthermore, in contrast to the present study, Ballard et al. (2019) found prey capture attempts, as recorded by wiggles, were strongly correlated with intermediate levels of light. Clearly, there are inter-colony differences in diurnal foraging behaviour and activity, although the processes driving these differential strategies remains an open question. Irrespective of solar light, underwater illuminance will vary based on local sea-ice cover and turbidity. Inter-colony differences in diurnal foraging activity may also be driven by diel vertical migration of the local prey field (Ainley & Ballard 2012, Ballard et al. 2019, Saenz et al. 2020). To investigate this further, future studies will need to examine diurnal foraging patterns within the context of these complex environmental considerations.

### 4.3. Stage- and sex-specific foraging patterns

As expected, there was a marked increase in diving effort over time from guard to crèche, which mirrors a larger foraging range (Clarke et al. 2006). During crèche, adults forage at sea simultaneously and can spend a longer time away from nests (Clarke et al. 2006). Extending foraging trip durations allowed individuals time to perform more foraging dives, and as a function of this, individuals covered a greater vertical distance, executed a greater number of wiggles and performed more foraging bouts (Table 5). An increase in foraging effort from guard to crèche, as evidenced by trip duration and meal mass, has been a consistently documented feature at Béchervaise Island (Clarke 2001, Clarke et al. 2006, Nicol et al. 2008, Tierney et al. 2009) and a number of other colonies (Ainley et al. 1998, Kato et al. 2003, Lyver et al. 2011). This increase in total foraging effort likely corresponds to a higher rate of prey capture to support the increasing energetic demands of chicks and self-maintenance requirements (Bost et al. 2007, Halsey et al. 2010, Takahashi et al. 2018).

We found that trip-level foraging efforts were particularly pronounced for males. This is a function of sex- and stage-related differences in trip duration, with males conducting relatively short trips in guard and much longer trips in crèche. These strategies are likely driven by physiological condition. At the beginning of guard, males are generally in better condition than females, having surplus energy reserves from their recent incubation foraging trip (Clarke 2001). Males take advantage of their heightened physical condition in guard to forage intensively, and solely for the purpose of provisioning chicks rather than for self-maintenance (Clarke 2001, Tierney et al. 2009). During guard, males exploit local nearshore foraging grounds and target pelagic fish (Tierney et al. 2009). In contrast, females forage further offshore where *E. superba* are an abun-

dant, reliable and an easily acquired source of energy (Clarke et al. 1998, Clarke 2001, Nicol et al. 2008, Tierney et al. 2009). Consistent with the breakdown of sea ice adjacent to the breeding colony, both adults forage at more distant locations in crèche (Clarke et al. 2006). Despite a greater level of dietary

Table 5. Summary of the relationships between trip-, bout- and dive-level parameters, sex (females and males) and stage (guard and crèche). Blue (red) arrows illustrate a positive (negative) association, with double arrow symbols indicating a more pronounced change between stages; cf: compared to. Equal signs indicate no significant relationship between sex or stage. Full coefficient results are provided in Section 3. See Table 1 for definitions and units of derived diving parameters

| Temporal scale | Observed changes in relation to sex and stage | |
| --- | --- | --- |
| | Females | Males |
| **Trip level** | | |
| Foraging trip duration | ↑ crèche | ↑↑ crèche |
| Dives per foraging trip | ↑ crèche | ↑↑ crèche |
| Vertical distance travelled | ↑ crèche | ↑↑ crèche |
| Number of wiggles | ↑ crèche | ↑↑ crèche |
| Vertical dive rate | | ↑ cf females |
| Proportion of bottom time | = = | = = |
| $ACPUE_t$ | = = | = = |
| Dive frequency | = = | = = |
| **Bout level** | | |
| Total number of bouts | ↑ crèche | ↑↑ crèche |
| Dives per bout | = = | = = |
| Proportion of dives in bouts (%) | ↑ crèche | ↓ crèche |
| **Dive level** | | |
| Dive depth | ↑ crèche | ↓ crèche |
| Dive duration | ↑ crèche | ↓ crèche |
| Bottom duration | ↑ crèche | ↓ crèche |
| Number of wiggles per dive | ↓ crèche | ↓ crèche |
| $ACPUE_d$ | ↓↓ crèche | ↓ crèche |

plasticity in crèche, there is evidence that males continue to consume more fish than females (Tierney et al. 2009). Our results show males spend a longer time at sea foraging in crèche. Similar to multiple colonies in the Ross Sea (Lescroël et al. 2010, Ainley et al. 2015), our findings suggest that nearshore fish resources may be depleted during guard, forcing males to seek out prey-rich locations further from the colony. This is a reasonable expectation for Adélie penguins at Béchervaise Island, given it is a small sub-colony within the broader Mawson region, which was home to approximately 100 000 pairs breeding in 2010 (Southwell et al. 2015).

Despite the differences in foraging effort described above, we found little evidence to suggest foraging intensity varied between sex or stage. Throughout the chick-rearing period, dives were performed with the same frequency, and no difference in the proportion of bottom time or $ACPUE_t$ were recorded. Furthermore, the number of dives comprising a bout were consistent between guard and crèche (Table 5). It has been suggested that males invest more time at the colony defending their chicks, thereby maximising foraging effort per unit time (Lescroël et al. 2019). We did not find strong evidence to support this sex difference in foraging effort per unit time. Temporal variation in foraging intensity is generally attributed to intra- and inter-specific competition stemming from prey dynamics, which are highly variable between colonies. For colonies in the Ross Sea, both higher (Lescroël et al. 2010) and lower (Lyver et al. 2011) foraging intensity (measured by foraging efficiency and dive frequency, respectively) has been recorded as the chick-rearing season progresses. Consistent with Lyver et al. (2011), we propose that Adélie penguins at Béchervaise Island respond to nearshore prey depletion and increased chick provisioning demands by expanding foraging range and duration rather than foraging intensity and effort per unit of time.

Substantial evidence indicates that sexes adopt differential diving behaviours, which also vary between guard and crèche. At Béchervaise Island, male dives were more structured in bouts during guard, although this sex pattern reversed in crèche. This likely suggests temporal variation in the structure and persistence of prey concentrations over the chick-rearing period (Watanabe et al. 2014). The complex dive-level patterns in relation to sex and stage supports this idea. For females, dive depths marginally increased in crèche; however, unexpectedly, our results show that bottom time also increased while $ACPUE_d$ decreased. On the other hand, males performed shallower dives in crèche with a marginally decreased bottom time and $ACPUE_d$. For both sexes, the number of wiggles per dive decreased in crèche (Table 5). These findings are inconsistent associations between dive profile characteristics, which suggests that bottom time and the number of wiggles should increase as dives become shallower. One explanation for this is that fine-scale dive profile information is confounded by extrinsic factors which cannot be reconciled using TDR data alone. This may include how penguin foraging behaviour is influenced by sea-ice conditions, bathymetry and the distribution, aggregation, locomotion and predator-avoidance techniques of preferred prey types (Charrassin et al. 2002, Kato et al. 2009, Halsey et al. 2010). It is difficult to disentangle complex dive behaviour without this complementary environmental information.

Our trip-, bout- and dive-level movement findings reinforce previously documented sex-specific differences in foraging strategies of chick-rearing Adélie penguins, although the precise mechanisms underlying this variation in dive characteristics remain unknown. The contrasting patterns in diving activity documented here are a likely response to inter- and intra-annual variation in prey distribution, availability and accessibility as the chick-rearing season progresses (Emmerson et al. 2015). Seasonal changes in prey biomass in the Mawson region have previously been demonstrated by repeat acoustic surveys (Nicol et al. 2008). Additionally, in the Ross Sea, predation pressure exerted by Adélie penguins and other marine predators drives changes in the vertical distribution of fish and krill, which corresponds to changes in penguin diving behaviour (Ainley et al. 2015). Seasonally fluctuating prey dynamics may help explain differential foraging strategies for male and female Adélie penguins at Béchervaise Island between chick-rearing stages. Furthermore, there is a seasonal reduction in the amount of sea ice present adjacent the Béchervaise Island breeding colony as the crèche period progresses. The region is primarily composed of fast-ice during guard, and breaks into a combination of fast- and pack-ice during crèche (Clarke et al. 2006, Emmerson et al. 2011, 2015). In East Antarctica, sea-ice cover is more extensive than in other regions around the continent. While the timing and extent of the diminution of sea ice is variable between years, these environmental dynamics can offer a variety of different foraging scenarios and may have a profound influence on how sexes modify their fish or krill predation strategies. Predatory tactics, and prey distribution and aggregation likely vary in relation to sea-ice conditions (Watanabe &

Takahashi 2013, Emmerson et al. 2015, Saenz et al. 2020). At Béchervaise Island, several studies have examined the effect of sea-ice cover on foraging tip duration (Clarke et al. 2002, Emmerson & Southwell 2008, Emmerson et al. 2015); however, it is unclear how these seasonal environmental dynamics are expected to influence bout- and dive-level behaviour. While it is clear that further directed research is needed to determine the temporal diving characteristics associated with fish or krill predation for Adélie penguins, our findings support evidence for sexual segregation in diet and differential provisioning roles between chick-rearing stages.

It is plausible that the sex-specific diving patterns recorded here are a function of males and females targeting different foraging grounds where predictable fish and krill prey fields are located (Kato et al. 2003). Static bathymetric features, such as shelf breaks and submarine canyons, influence local upwelling and prey distribution, acting as foraging hotspots for higher predators (Kokubun et al. 2015). While investigating the horizontal movements of breeding Adélie penguins at Béchervaise Island, Clarke et al. (2006) found evidence to suggest foraging in close association with these bathymetric features, although the possibility of sex-specific selection of foraging sites was not explored. Segregation in foraging habitat between sexes was demonstrated for breeding Adélie penguins at Dumont d'Urville in East Antarctica (Widmann et al. 2015). Our comprehensive treatment of the vertical dimension will lay strong foundations for upcoming work integrating data from both the horizontal and vertical dimensions to identify key foraging areas.

## 4.4. Conclusions

The chick-rearing months are times of intense foraging pressures for breeding Adélie penguins. Foraging success during these months is critical to reproductive success and chick survival. Our results indicate that the diving efforts of chick-rearing Adélie penguins varies considerably over time from guard to crèche according to changes in life history requirements. There were marked sex-specific differences in diving behaviour which are consistent with proposed variations in diet and foraging strategies between sexes. We also found evidence indicating diurnal patterns in diving behaviour. Our findings highlight the utility of examining the foraging behaviour of diving marine predators at multiple scales. While this study represents an important first

step in characterising dive behaviour at Béchervaise Island, further research is needed to understand how dive characteristics are linked to feeding events, sea-ice conditions and the visual prey field. Unravelling the complex relationships between environmental conditions and spatiotemporal patterns in Adélie penguin foraging movements and habitat selection will advance our understanding of functional predator–prey relationships and population-level foraging behaviour.

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