

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

Running page head: **Diving behaviour of Adélie penguins**

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# 1 ABSTRACT

2 Breeding Adélie penguins forage at sea and return to land to provision their chicks,  
3 adjusting their foraging behaviour in response to environmental fluctuations over time. At  
4 Béchervaise Island, a nesting site in an East Antarctic population, Adélie penguin diving  
5 behaviour remains undocumented. This represents a key area of uncertainty in efforts to  
6 understand and predict foraging success at this colony. Here, we compile a multi-year telemetry  
7 dataset from time-depth recorders deployed from 1992-2004 on 64 birds at Béchervaise Island.  
8 We examine diving activity at multiple scales: ranging from foraging trips (n=125) to dive bouts  
9 (n=3461) to individual dives (n=84,521). We characterise the stage- and sex-specific variation  
10 in diving behaviour of chick-rearing Adélie penguins using linear mixed effect models. Total  
11 foraging trip effort (trip duration, number of dives, vertical distance travelled and number of  
12 wiggles) substantially increased as the chick-rearing period progressed (guard through crèche),  
13 consistent with increasing chick provisioning and self-maintenance requirements over time.  
14 Foraging activity was predominantly structured in periods of sustained diving bouts, indicating  
15 sustained foraging effort over the course of the foraging trip. Diving behaviour (dive-level  
16 depth, duration, bottom time and ACPUE<sub>d</sub>) varied in relation to sex and chick-rearing stage.  
17 Dives were performed more frequently during high and low levels of solar light which is likely  
18 linked to visual predation strategies or prey activity. Our findings advance our understanding  
19 of this population's foraging behaviour, which is ultimately required to underpin the  
20 conservation and management of this breeding colony.

# 1 INTRODUCTION

Adélie penguins (*Pygoscelis adeliae*) have a circumpolar distribution and are one of the most extensively studied Southern Ocean predators (Ainley 2002, Ancel et al. 2013). This seabird has 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 function of these ecological attributes, Adélie penguins are a species which 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 one of the key study species under the Commission for the Conservation of Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP) (Agnew 1997, Ainley 2002).

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, Ropert-Coudert et al. 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 three-dimensional, heterogeneous marine environment and returning to the colony to assume incubation duties or feed their chicks.

1 Foraging effort comprises movement in both the horizontal and vertical dimensions (Ainley  
2 2002). Knowledge gaps in relation to these vertical and horizontal foraging components, and  
3 how they relate to the prey-field and sea-ice conditions, represents a key area of uncertainty in  
4 efforts to understand and predict foraging success (Emmerson et al. 2015, Takahashi et al. 2018,  
5 Saenz et al. 2020).

6 For Adélie penguins, diving is a fundamental component of foraging and acquiring  
7 energy. Foraging effort is amplified during the breeding season, when breeding pairs must  
8 acquire energy for themselves and their chicks (Ainley 2002, Thiebot et al. 2019). During this  
9 period, diving movements are constrained by a variety of intrinsic and extrinsic factors. Intrinsic  
10 constraints include basic self-maintenance necessities, physiological condition and  
11 requirements to return to the colony to provision chicks. Extrinsic constraints include proximity  
12 of forage grounds to nesting sites, physical barriers posed by sea ice, and levels of biological  
13 productivity influencing prey abundance (Lescroël et al. 2010, Emmerson et al. 2015, Saenz et  
14 al. 2020). Adélie penguins are known to change their foraging behaviour during the breeding  
15 cycle in response to environmental variability, fluctuations in the prey-field, parental body  
16 condition and chick provisioning requirements over time (Clarke et al. 2006, Tierney et al.  
17 2009, Ballard et al. 2010). Determining how these intrinsic and extrinsic factors shape diving  
18 behaviours and success can yield insight into how Adélie penguin populations may respond to  
19 seasonal and inter-annual changes in prey availability, and environmental change more broadly  
20 (Emmerson et al. 2015, Le Guen et al. 2018, Takahashi et al. 2018).

21 Diving activity of chick-rearing Adélie penguins has been reported in East Antarctica  
22 at Lützow-Holm Bay (Kato et al. 2003, Watanuki et al. 2010), Prydz Bay (Whitehead 1989,  
23 Watanuki et al. 1997) and Dumont d’Urville (Rodary et al. 2000, Ropert-Coudert et al. 2002,  
24 Le Guen et al. 2018), as well as colonies in the Ross Sea (Lescroël et al. 2010, Nesti et al. 2010,  
25 Lyver et al. 2011, Ainley et al. 2015, Ford et al. 2015, Lescroël et al. 2020) and the Antarctica  
26 Peninsula (Chappell et al. 1993). However, many studies have been restricted by sampling over  
27 limited temporal scales, with few comparing diving activity between the two chick-rearing

1 stages; guard and crèche (Rodary et al. 2000, Lescroël et al. 2010, Nesti et al. 2010, Lyver et  
2 al. 2011). Furthermore, substantial inter-colony differences are evident in Adélie penguin  
3 foraging behaviour, driven by regional variation in physical and environmental features, prey  
4 distribution, and intra- and inter-specific competition (Lescroël et al. 2010, Watanuki et al.  
5 2010, Ford et al. 2015). To better understand how diving effort changes throughout the chick-  
6 rearing season, there is a need to examine colony-specific diving activity across a range of  
7 temporal scales.

8 In this study, we examine the historical dive data available for the Béchervaise Island  
9 Adélie penguin colony to determine how diving behaviour varies between males and females  
10 through the chick-rearing period. Compiling an extensive multi-year telemetry dataset from  
11 bird-attached time-depth recorders, we analyse a suite of diving parameters calculated during  
12 the guard and crèche stages. Temporal patterns and sex-specific variation in diving behaviour  
13 is characterised at multiple scales: ranging from foraging trips to diving bouts to individual  
14 dives. In quantifying vertical movements across these three scales, we expected (1) total and  
15 per unit time foraging effort would increase from guard to crèche, (2) males and females would  
16 exhibit markedly different foraging behaviour between chick-rearing stages, and (3) diurnal  
17 patterns in foraging behaviour would be evident, assuming solar light influences visual  
18 predation strategies and prey vertical migrations. Our findings are discussed within the context  
19 of life history constraints and intraspecific diet variability, and the future outlook towards  
20 integrating diving behaviour with spatial movement and environmental information to assess  
21 spatiotemporal patterns of forage resources used by this colony.

## 23 **2 MATERIALS & METHODS**

### 24 *2.1 Instrument deployment and processing of dive data*

25 Adélie penguins have been a focus of long-term monitoring at Béchervaise Island  
26 (67°35 S, 67°49 E), a designated CEMP site since 1990. Béchervaise Island is a nesting site  
27 which is part of an East Antarctic colony, with over 2000 breeding pairs (Kerry et al. 2000).

Time-depth recorders (TDRs) were deployed over the breeding seasons between 1992-93 and 2003-04 and cover both stages of the chick-rearing period: guard (late-December to mid-late-January) and crèche (mid-January to early-mid-February) (Ainley 2002). Here, we collate dive data over the course of 10 breeding seasons (excluding the 1997-1998 and 1999-2000 seasons in which data was not retrieved or useable). The dive records in this study represent 64 penguins over 125 different foraging trips (Fig. 1; Table S1 in the supplementary material).

Breeding individuals were captured at nests and their breeding status and weight 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 secured with cable ties threaded under the feathers and around the device. Individual birds carried TDRs for one to six 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 two different TDR models. Wildlife Computers Mk5 TDRs (Redmond, USA) were used for four breeding seasons between 1992 and 1999. These weighed 50 g, measured 65 x 35 x 15 mm and recorded depth in 5, 2 or 1 s increments with a  $\pm 1$  m resolution. From the year 2000 onwards Mk7 TDRs were deployed. These devices weighed 30 g, measured 98.5 x 20 x 10 mm and recorded depth every 1 s with a  $\pm 0.5$  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 in Clarke et al. (2002). TDRs were fitted to penguins already carrying an implanted, individually unique, electronic identification tag (Clarke & Kerry 1994).

Archived dive data was 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 statistical software 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-year 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 foraging 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, have been shown to 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 in 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 differences 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 seconds were removed. The bout ending criterion (BEC) was first determined for males and females separately, which were estimated as 295 and 282 seconds respectively. Given the minor difference (<10 sec) in sex-specific BEC values, data was pooled and a single BEC value generated for all individuals, which was 288 seconds. Post-dive surface intervals greater than 288 seconds 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 two wiggle metrics (excluding 5 and 2 s TDR sampling rates); number of wiggles per dive and attempts of catch per unit effort (ACPUE<sub>d</sub>) (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 2013). Given 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 timestamp 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 models (LMMs) were fitted separately for trip-, bout- and dive-level foraging analyses (*lme* function, *nlme* package; Pinheiro et al. 2016). 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<sub>d</sub> 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 performed using

Akaike's information criterion (AIC). All dive-level LMMs were fit with a temporal autocorrelation term (corCAR1) 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 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 in the supplementary material).

#### 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 hours in guard, and 96 and 66 hours in crèche, for males and females respectively (See Table 2 for means and 95% CI). Dive frequency,  $ACPUE_t$  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 being significantly more pronounced for males. The same pattern was observed for the total number of dives, total vertical distance travelled and total number of wiggles (Fig. 2; Table S2 in the supplementary material 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 to crèche that was more pronounced for males (Fig. 3; Table S3 in the supplementary material 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; Table S3 in the supplementary material for full model results).

### *3.3 Dive-level*

Across the 84,521 recorded foraging dives, the maximum dive depth recorded by TDRs was 115 m 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 in the supplementary material). The mean dive depths were near to 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 show 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, however bottom duration was also marginally reduced. In contrast, females dived to similar depths throughout the chick-rearing period, however dives in crèche had a longer bottom phase and duration. The number of wiggles per dive was positively correlated with dive bottom duration and ACPUE<sub>d</sub> 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; Table S4 in the supplementary material 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; Table S4 in the supplementary material 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 higher 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  $-6.24^\circ$  and  $45.71^\circ$ , never dipping below nautical twilight (i.e.,  $12^\circ$  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 the dives recorded, 37.5% took place during the dawn period ( $<12^\circ$  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 Adélie penguins’ underwater foraging behaviour and are generally consistent with the sex-specific foraging strategies identified throughout the chick-rearing period at Béchervaise Island (Clarke et al. 1998, Clarke et al. 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 metres of the water column. These diving patterns are consistent with observations from other locations in East Antarctica, such as Lützow-Holm Bay and Dumont d'Urville (Ropert-Coudert et al. 2001, Kato et al. 2003, Kato et al. 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 (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.

1           However, a high degree of bout activity need not exclusively correspond to a model of  
2 commuting to, and foraging within, prey patches in a heterogeneous prey-field. Similar to  
3 Adélie penguins in the Ross Sea (Ford et al. 2015), sustained bout activity for the Béchervaise  
4 Island population may reflect high prey availability relative to their rate of consumption. This  
5 could be driven by horizontal and vertical transport restoring prey abundance, or alternatively,  
6 penguins continuously and opportunistically foraging over the course of the foraging trip (Ford  
7 et al. 2015). Our findings of no sex- or stage-related difference in the number of dives  
8 comprising a bout supports this idea, suggesting the temporal organisation of foraging dives  
9 within a foraging bout, is limited by physiological constraints rather than prey availability (Ford  
10 et al. 2015). Further information on penguin horizontal-vertical movement relationships, and  
11 how this relates to regional prey-field characteristics, are needed to validate these  
12 interpretations about bout diving activity for Adélie penguins at this colony.

13           Wiggles are commonly used as a metric of foraging behaviour for penguins and other  
14 diving marine predators to infer prey capture attempts (Roncon et al. 2018). For Adélie  
15 penguins at Béchervaise Island, an increased number of wiggles corresponded to increased time  
16 spent in the bottom phase of dives. This indicates most prey capture attempts likely occurred in  
17 the bottom phase of dives (Bost et al. 2007). We also found that an increased amount of time  
18 spent in the bottom phase corresponded with a longer total dive duration. Conversely,  
19 increasing dive depth was associated with a reduced bottom time. These results may be a  
20 function of optimal foraging strategies in the context of breath-holding limitations (Chappell et  
21 al. 1993). Travelling to depths generally has a greater cost on energy and oxygen reserves,  
22 particularly for smaller divers, therefore reducing the proportion of dive time which can be  
23 dedicated to foraging. Hence, prey capture attempts can be maximised during shallow feeding  
24 opportunities. This has interesting implications when considering the role of sea-ice in  
25 aggregating shallow prey (Nicol 2006), and potentially creating a floor-like barrier or ceiling  
26 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 are known 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 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 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 the 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 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



1 physiological condition. At the beginning of guard, males are generally in better condition than  
2 females, having surplus energy reserves from their recent incubation foraging trip (Clarke  
3 2001). Males take advantage of their heightened physical condition in guard to forage  
4 intensively, and solely for the purpose of provisioning chicks rather than for self-maintenance  
5 (Clarke 2001, Tierney et al. 2009). During guard, males are known to exploit local nearshore  
6 foraging grounds and target pelagic fish (Tierney et al. 2009). In contrast, females forage further  
7 offshore where *E. superba* are an abundant, reliable and an easily acquired source of energy  
8 (Clarke et al. 1998, Clarke 2001, Nicol et al. 2008, Tierney et al. 2009). Consistent with the  
9 breakdown of sea ice adjacent the breeding colony, both adults forage at more distant locations  
10 in crèche (Clarke et al. 2006). Despite a greater level of dietary plasticity in crèche, there is  
11 evidence males continue to consume more fish than females (Tierney et al. 2009). Our results  
12 show males spend a longer time at sea foraging in crèche. Similar to multiple colonies in the  
13 Ross Sea (Lescroël et al. 2010, Ainley et al. 2015), our findings suggest nearshore fish resources  
14 may be depleted during guard, forcing males to seek out prey-rich locations further from the  
15 colony. This is a reasonable expectation for Adélie penguins at Béchervaise Island, given it is  
16 a small sub colony within the broader Mawson region, which was home to approximately  
17 100,000 pairs breeding in 2010 (Southwell et al. 2015).

18         Despite the differences in foraging effort described above, we found little evidence to  
19 suggest foraging intensity varied between sex or stage. Throughout the chick-rearing period,  
20 dives were performed with the same frequency, and no difference in the proportion of bottom  
21 time or ACPUE<sub>t</sub> were recorded. Furthermore, the number of dives comprising a bout were  
22 consistent between guard and crèche (Table 5). It has been suggested males invest a greater  
23 time at the colony defending their chicks, thereby maximising foraging effort per unit time  
24 (Lescroël et al. 2019). We did not find strong evidence to support this sex difference in per unit  
25 time foraging effort. Temporal variation in foraging intensity is generally attributed to intra-  
26 and inter-specific competition stemming from prey dynamics, which is highly variable between  
27 colonies. For colonies in the Ross Sea, both a 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 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 per unit of time effort.

There is substantial evidence sexes adopt differential diving behaviours, which also varies 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 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). It must be noted these findings are inconsistent associations between dive profile characteristics, which suggests 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 for chick-rearing Adélie penguins, although the precise mechanisms underlying this variation in dive characteristics remains unknown. The contrasting patterns in diving activity documented here are a likely response to inter- and intra-

1 annual variation in prey distribution, availability and accessibility as the chick-rearing season  
2 progresses (Emmerson et al. 2015). Seasonal changes in prey biomass in the Mawson region  
3 have previously been demonstrated by repeat acoustic surveys (Nicol et al. 2008). Additionally,  
4 in the Ross Sea, predation pressure exerted by Adélie penguins and other marine predators  
5 drives changes in the vertical distribution of fish and krill, which corresponds to changes in  
6 penguin diving behaviour (Ainley et al. 2015). Seasonally fluctuating prey dynamics may help  
7 explain differential foraging strategies for male and female Adélie penguins at Béchervaise  
8 Island between chick-rearing stages. Furthermore, there is a seasonal reduction in the amount  
9 of sea ice present adjacent the Béchervaise Island breeding colony as the crèche period  
10 progresses. The region is primarily composed of fast-ice during guard, and breaks into a  
11 combination of fast- and pack-ice during crèche (Clarke et al. 2006, Emmerson et al. 2011,  
12 Emmerson et al. 2015). In East Antarctica, sea-ice cover is more extensive than other regions  
13 around the continent. While the timing and extent of the diminution of sea ice is variable  
14 between years, these environmental dynamics can offer a variety of different foraging scenarios  
15 and may have a profound influence on how sexes modify their fish or krill predation strategies.  
16 Predatory tactics, and prey distribution and aggregation likely varies in relation to sea-ice  
17 conditions (Watanabe & Takahashi 2013, Emmerson et al. 2015, Saenz et al. 2020). At  
18 Béchervaise Island, several studies have examined the effect of sea-ice cover on foraging tip  
19 duration (Clarke et al. 2002, Emmerson & Southwell 2008, Emmerson et al. 2015), however it  
20 is unclear how these seasonal environmental dynamics are expected to influence bout- and dive-  
21 level behaviour. While it is clear further directed research is needed to determine the temporal  
22 diving characteristics associated with fish or krill predation for Adélie penguins, our findings  
23 support evidence for sexual segregation in diet and differential provisioning roles between  
24 chick-rearing stages.

25         It is plausible that the sex-specific diving patterns recorded here are a function of males  
26 and females targeting different foraging grounds where predictable fish and krill prey-fields are  
27 located (Kato et al. 2003). Static bathymetric features, such as the shelf break 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, however 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 works integrating data from both the horizontal and vertical dimensions to identify key foraging areas.

## 5 CONCLUSION

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 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 is consistent with proposed variation 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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9

# 1 Tables

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

| Derived diving metrics   | Calculation  | Explanation  | Examples of usage   |
|--|--|--|---|
| <b>Trip-level derived metrics calculated from dive information</b> |  |  |   |
| Dive frequency   | $\frac{\text{Number of dives per foraging trip}}{\text{Foraging trip duration}}$                       | Number of dives per unit of time (here, dives per hour).   | Staniland et al. (2010), Antarctic fur seals.   |
| Vertical dive rate   | $\frac{\text{Vertical distance travelled}}{\text{Foraging trip duration}}$                             | Total sum of the maximum dive depth of each individual dive divided by the total trip duration (here, km per hour).            | Zimmer et al. (2008b), Emperor penguins; Pütz et al. (2006), Southern rockhopper penguins |
| Proportion of bottom time  | $\frac{\text{Total time spent in bottom duration}}{\text{Total time submerged}}$                       | 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 <sub>t</sub> )            | $\frac{\text{Total number of wiggles}}{\text{Total time in bottom duration}}$                          | 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            |
| <b>Bout-level derived metrics calculated from dive information</b> |  |  |   |
| Proportion of dives in bouts                                       | $\frac{\text{Number of bout dives per foraging trip}}{\text{Total number of dives per foraging trip}}$ | Proportion of the total dive number allocated as bout diving.  | Lea et al. (2002), Luque et al. (2008), Antarctic fur seals.                              |
| <b>Dive-level derived metrics calculated from dive information</b> |  |  |   |
| ACPUE <sub>d</sub>   | $\frac{\text{Number of wiggles}}{\text{Bottom duration}}$  | Number of prey capture attempts (with or without success) relative to individual bottom duration.                              | Refer to trip-level ACPUE above.  |

4

5

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

| Number of birds = 64<br>Diving Parameter   | Guard<br>(n = 90 trips)  |                        | Crèche<br>(n = 35 trips) |                        |
|--|--------------------------|------------------------|--------------------------|------------------------|
|  | Female<br>(n = 40 trips) | Male<br>(n = 50 trips) | Female<br>(n = 15 trips) | Male<br>(n = 20 trips) |
| Foraging trip duration (hours)             | 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 <sup>-1</sup> )    | 312 (122-798)            | 410 (138-1218)         | 354 (133-940)            | 382 (187-781)          |
| Proportion of bottom time                  | 0.49 $\pm$ 0.10          | 0.48 $\pm$ 0.11        | 0.46 $\pm$ 0.09          | 0.50 $\pm$ 0.08        |
| ACPUE <sub>t</sub> %                       | 15 (6-36)                | 14 (6-35)              | 16 (8-31)                | 17 (11-28)             |
| Foraging dive frequency (h <sup>-1</sup> ) | 15 (8-31)                | 15 (8-29)              | 16 (9-26)                | 16 (9-30)              |

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2 Table 3. Bout-level summaries of Adélie penguins foraging at Béchervaise Island (n = 64 birds, n =  
3 125 trips, n = 3,461 bouts). Proportion of dives in bouts, which was logit transformed in linear mixed  
4 effects models, is presented as an arithmetic mean  $\pm$  standard deviation. All other metrics are  
5 presented as geometric means (95% confidence interval). See *Methods* for details of data  
6 transformations. Results presented as in Table 2.

| Number of birds = 64<br><br>Diving Parameter | Guard<br>(n = 90 trips)  |                        | Crèche<br>(n = 35 trips) |                        |
|--|--------------------------|------------------------|--------------------------|------------------------|
|  | Female<br>(n = 40 trips) | Male<br>(n = 50 trips) | Female<br>(n = 15 trips) | Male<br>(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 $\pm$ 0.16          | 0.75 $\pm$ 0.13        | 0.75 $\pm$ 0.14          | 0.73 $\pm$ 0.11        |

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2 Table 4. Dive-level summaries of Adélie penguins foraging at Béchervaise Island (n = 64 birds, n =  
3 125 trips). All metrics are presented as geometric means (95% confidence interval). See *Methods* for  
4 details of data transformations. Results presented as in Table 2.

| Number of birds = 64<br><br>Diving Parameter | Guard<br>(n = 90 trips)  |                        | Crèche<br>(n = 35 trips) |                        |
|--|--------------------------|------------------------|--------------------------|------------------------|
|  | Female<br>(n = 40 trips) | Male<br>(n = 50 trips) | Female<br>(n = 15 trips) | Male<br>(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 <sub>d</sub> per dive %                | 15 (5-48)                | 15 (5-48)              | 16 (5-48)                | 17 (5-50)              |

5

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

| Temporal scale                   | Observed changes in relation to sex and stage |              |
|----------------------------------|---|--------------|
|                                  | Females                                       | Males        |
| <b>Trip-level</b>                |   |              |
| 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 <sub>t</sub>               | = =   | = =          |
| Dive frequency                   | = =   | = =          |
| <b>Bout-level</b>                |   |              |
| Total number of bouts            | ↑ crèche                                      | ↑↑ crèche    |
| Dives per bout                   | = =   | = =          |
| Proportion of dives in bouts (%) | ↑ crèche                                      | ↓ crèche     |
| <b>Dive-level</b>                |   |              |
| Dive depth                       | ↑ crèche                                      | ↓ crèche     |
| Dive duration                    | ↑ crèche                                      | ↓ crèche     |
| Bottom duration                  | ↑ crèche                                      | ↓ crèche     |
| Number of wiggles per dive       | ↓ crèche                                      | ↓ crèche     |
| ACPUE <sub>d</sub>               | ↓↓ crèche                                     | ↓ crèche     |



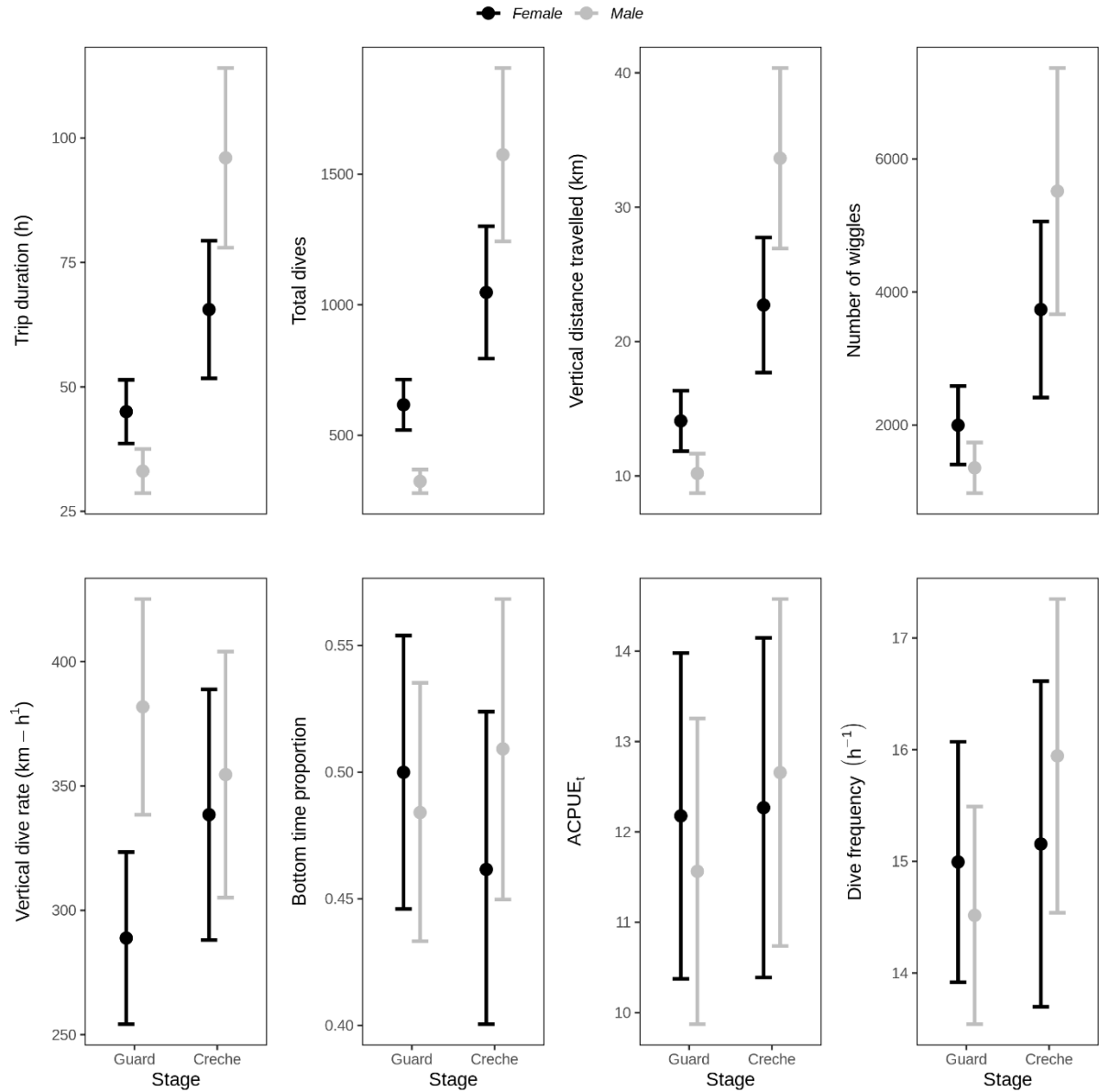
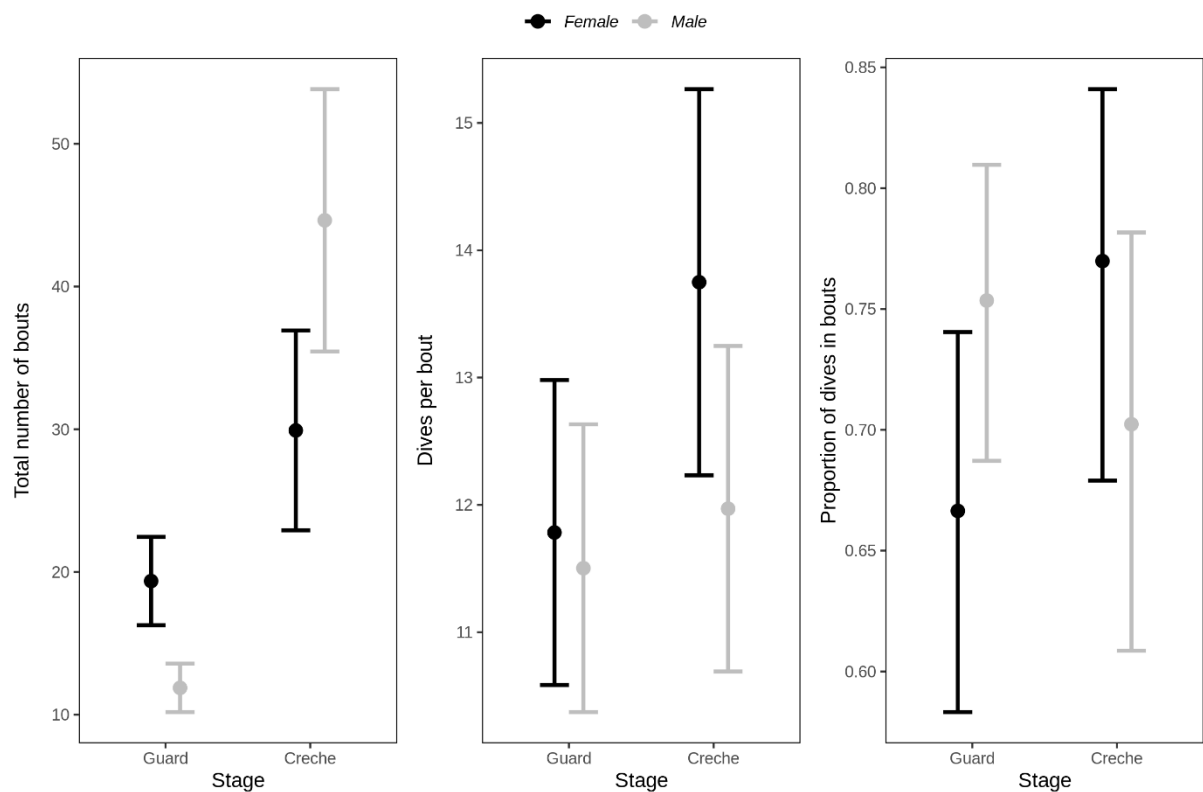


Fig. 2. Model results for trip-level diving parameters in relation to chick-rearing stage (guard and crèche) for females (black) and males (grey). Results are presented as the back-transformed estimated means (95% confidence intervals) from fitted linear mixed effects models, plotted using the *effects*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



1



2

3 Fig. 3. Model results for bout-level diving parameters in relation to chick-rearing stage (guard and  
4 crèche) for females (black) and males (grey). Results presented as back-transformed estimated means  
5 (95% confidence intervals) from fitted linear mixed effects models, as in Fig. 2. See Table 1 for  
6 definitions and units of derived diving parameters and Table S3 in the supplementary material for full  
7 model results.

8

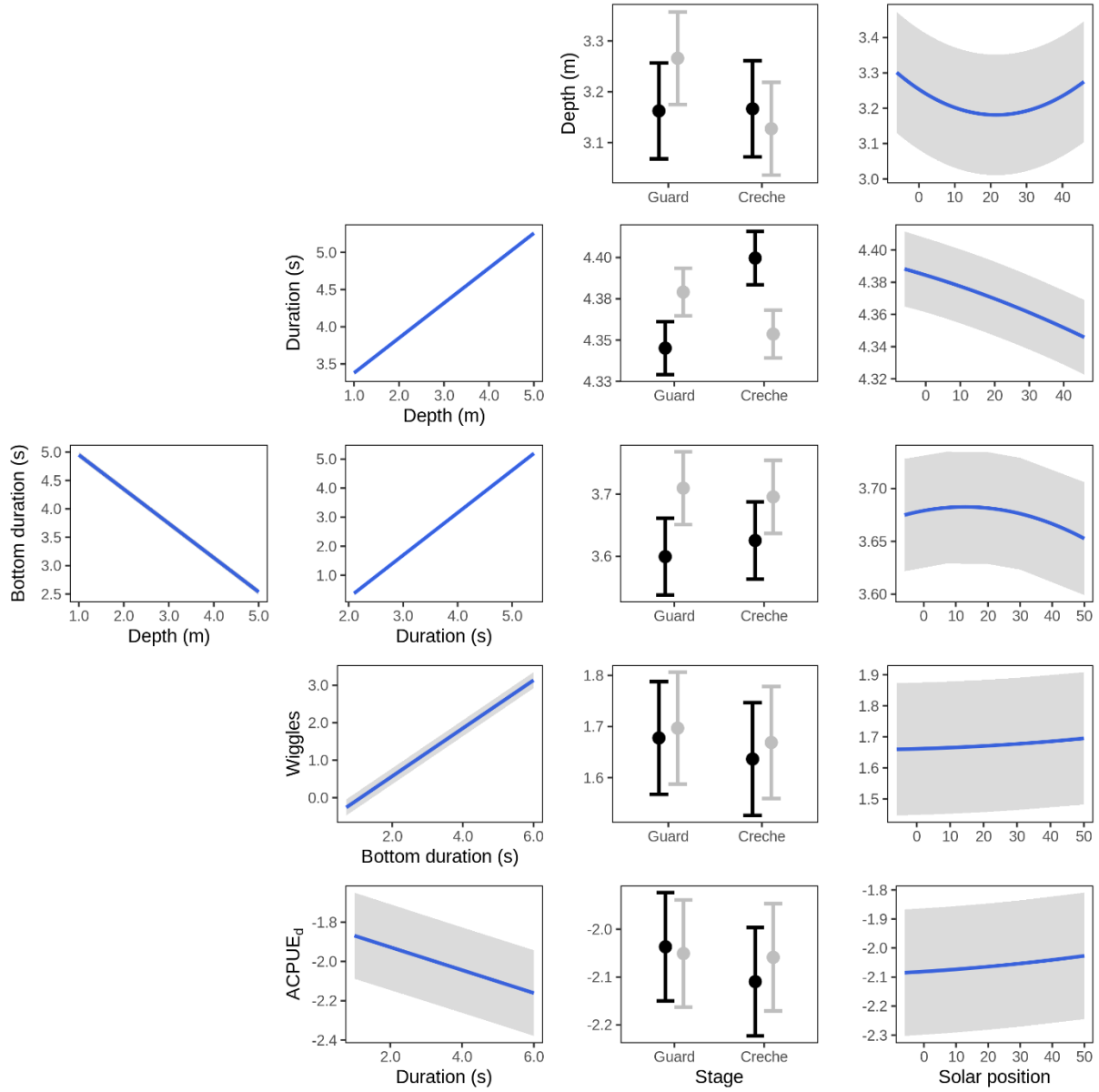


Fig. 4. Results for dive-level parameters modelled in relation to other dive parameters, chick-rearing stage (guard and creche), sex (females: black; males: grey) and solar position (quadratic term). The solid blue lines represent the regression fit to observations and the grey shaded area indicates the 95% confidence intervals (CIs). Tight CIs are not visible in panels displaying the relationship between diving parameters, with two exceptions (wiggles in relation to bottom duration and ACPUE<sub>d</sub> 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 in the supplementary material for full model results.

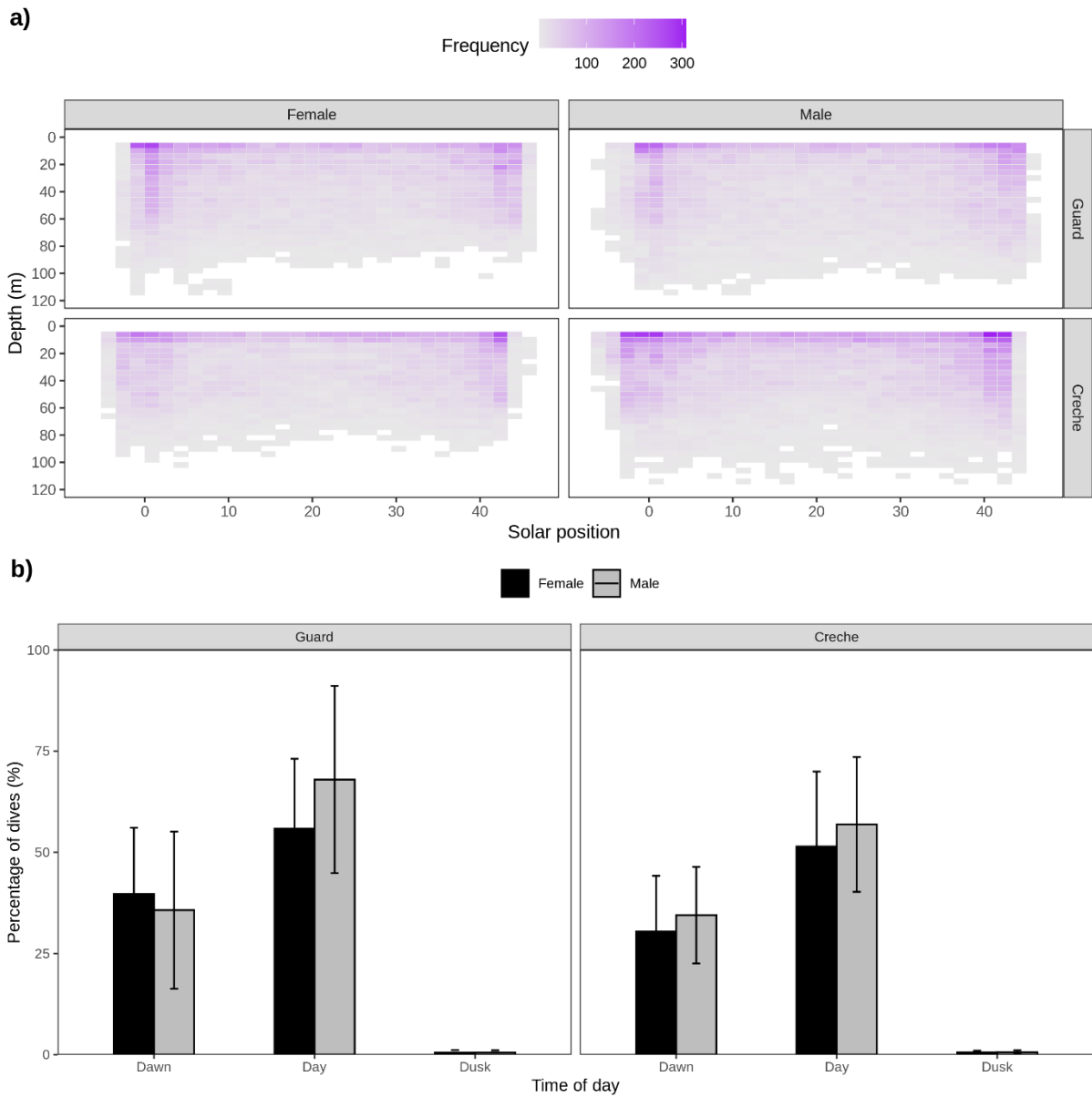


Fig. 5. Compiled TDR data showing the recorded observations of diurnal diving behaviour through time (total  $n = 64$  birds,  $n = 84,521$  foraging dives). Displayed is the (a) frequency diving activity in relation to depth and solar position, and b) percentage diving activity at times designated as dawn, day and dusk (see *Methods* for details of diurnal categories). Plots are separated by sex and stage.

# 1 Supplementary material

2 Table S1. Number of male and female penguins tracked from Béchervaise Island each year, presented  
3 alongside the number of foraging trips per season and chick-rearing period (guard and crèche).

|         |        | Birds | Total trips | Guard trips | Crèche trips |
|---------|--------|-------|-------------|-------------|--------------|
| 1992-93 | Female | 3     | 3           | 1           | 2            |
|         | Male   | 5     | 8           | 5           | 3            |
|         | Total  | 8     | 11          | 6           | 5            |
| 1993-94 | Female | 3     | 8           | 7           | 1            |
|         | Male   | 4     | 7           | 5           | 2            |
|         | Total  | 7     | 15          | 12          | 3            |
| 1994-95 | Female | 2     | 2           | 2           | 0            |
|         | Male   | 2     | 2           | 2           | 0            |
|         | Total  | 4     | 4           | 4           | 0            |
| 1995-96 | Female | 0     | 0           | 0           | 0            |
|         | Male   | 1     | 2           | 2           | 0            |
|         | Total  | 1     | 2           | 2           | 0            |
| 1996-97 | Female | 1     | 2           | 2           | 0            |
|         | Male   | 1     | 2           | 2           | 0            |
|         | Total  | 2     | 4           | 4           | 0            |
| 1998-99 | Female | 3     | 11          | 7           | 4            |
|         | Male   | 3     | 8           | 5           | 3            |
|         | Total  | 6     | 19          | 12          | 7            |
| 2000-01 | Female | 10    | 19          | 14          | 5            |
|         | Male   | 12    | 22          | 12          | 10           |
|         | Total  | 22    | 41          | 26          | 15           |
| 2001-02 | Female | 2     | 5           | 5           | 0            |
|         | Male   | 3     | 6           | 5           | 1            |
|         | Total  | 5     | 11          | 10          | 1            |
| 2002-03 | Female | 3     | 4           | 1           | 3            |
|         | Male   | 4     | 11          | 10          | 1            |
|         | Total  | 7     | 15          | 11          | 4            |
| 2003-04 | Female | 1     | 1           | 1           | 0            |
|         | Male   | 1     | 2           | 2           | 0            |
|         | Total  | 2     | 3           | 3           | 0            |
| Total   | Female | 28    | 55          | 40          | 15           |
|         | Male   | 36    | 70          | 50          | 20           |
|         | Total  | 64    | 125         | 90          | 35           |

Table S2. Results of linear mixed effects models for trip-level diving parameters in relation to sex and stage, allowing an interaction term. Estimated means  $\pm$  SE are presented on the natural log scale, and the logit scale for proportion of bottom time. See *Methods* and Table 1 for details of diving parameters and model fits. Note that females during guard are the reference level. Significant *p*-values are highlighted in bold text.

| Response variable                        | Predictor variable                 | Coefficients |      |                 |                   |
|--|------------------------------------|--------------|------|-----------------|-------------------|
|  |                                    | Est          | SE   | <i>t</i> -value | <i>p</i> -value   |
| Foraging trip duration (hours)           | Intercept                          | 3.80         | 0.14 | 26.82           | <b>&lt;0.0001</b> |
|  | Sex (male)                         | -0.31        | 0.18 | -1.72           | 0.68              |
|  | <b>Stage (crèche)</b>              | 0.38         | 0.23 | 1.61            | <b>&lt;0.0001</b> |
|  | <b>Sex (male) * Stage (crèche)</b> | 0.69         | 0.31 | 2.09            | <b>&lt;0.05</b>   |
| Dives per foraging trip                  | Intercept                          | 6.42         | 0.16 | 40.98           | <b>&lt;0.001</b>  |
|  | Sex (male)                         | -0.65        | 0.21 | -3.07           | 0.08              |
|  | <b>Stage (crèche)</b>              | 0.53         | 0.28 | 1.91            | <b>&lt;0.001</b>  |
|  | <b>Sex (male) * Stage (crèche)</b> | 1.05         | 0.37 | 2.84            | <b>&lt;0.01</b>   |
| Vertical distance travelled (km)         | Intercept                          | 2.64         | 0.16 | 16.60           | <b>&lt;0.001</b>  |
|  | Sex (male)                         | -0.32        | 0.20 | -1.64           | 0.64              |
|  | <b>Stage (crèche)</b>              | 0.48         | 0.24 | 1.99            | <b>&lt;0.001</b>  |
|  | <b>Sex (male) * Stage (crèche)</b> | 0.72         | 0.32 | 2.22            | <b>&lt;0.05</b>   |
| Number of wiggles                        | Intercept                          | 7.60         | 0.30 | 25.72           | <b>&lt;0.001</b>  |
|  | Sex (male)                         | -0.39        | 0.22 | -1.72           | 0.53              |
|  | <b>Stage (crèche)</b>              | 0.63         | 0.29 | 2.18            | <b>&lt;0.001</b>  |
|  | <b>Sex (male) * Stage (crèche)</b> | 0.78         | 0.39 | 2.01            | <b>&lt;0.05</b>   |
| Vertical dive rate (km h <sup>-1</sup> ) | Intercept                          | 5.67         | 0.12 | 47.28           | <b>&lt;0.001</b>  |
|  | <b>Sex (male)</b>                  | 0.28         | 0.18 | 2.38            | <b>&lt;0.05</b>   |
|  | Stage (crèche)                     | 0.16         | 0.14 | 1.16            | 0.74              |
|  | Sex (male) * Stage (crèche)        | -0.23        | 0.18 | -1.27           | 0.21              |
| Proportion of bottom time                | Intercept                          | -0.01        | 0.11 | -0.01           | 0.68              |
|  | Sex (male)                         | -0.06        | 0.87 | -0.73           | 0.83              |
|  | Stage (crèche)                     | -0.15        | 0.10 | -1.61           | 0.79              |
|  | Sex (male) * Stage (crèche)        | 0.25         | 0.13 | 1.96            | 0.06              |
| ACPUE <sub>t</sub>                       | Intercept                          | 2.50         | 0.15 | 16.88           | <b>&lt;0.001</b>  |
|  | Sex (male)                         | -0.05        | 0.05 | -1.11           | 0.55              |
|  | Stage (crèche)                     | 0.08         | 0.05 | 0.14            | 0.18              |
|  | Sex (male) * Stage (crèche)        | 0.08         | 0.07 | 1.15            | 0.26              |
| Dive frequency (h <sup>-1</sup> )        | Intercept                          | 2.70         | 0.07 | 37.70           | <b>&lt;0.001</b>  |
|  | Sex (male)                         | -0.03        | 0.08 | -0.42           | 0.94              |
|  | Stage (crèche)                     | 0.01         | 0.10 | 0.11            | 0.39              |
|  | Sex (male) * Stage (crèche)        | 0.08         | 0.13 | 0.63            | 0.53              |

- 1 Table S3. Results of linear mixed effects models for bout-level diving parameters in relation to sex  
2 and stage. Estimated means  $\pm$  SE are presented on the natural log scale, and the logit scale for  
3 proportion of dives in bout. Results presented as in Table S2.

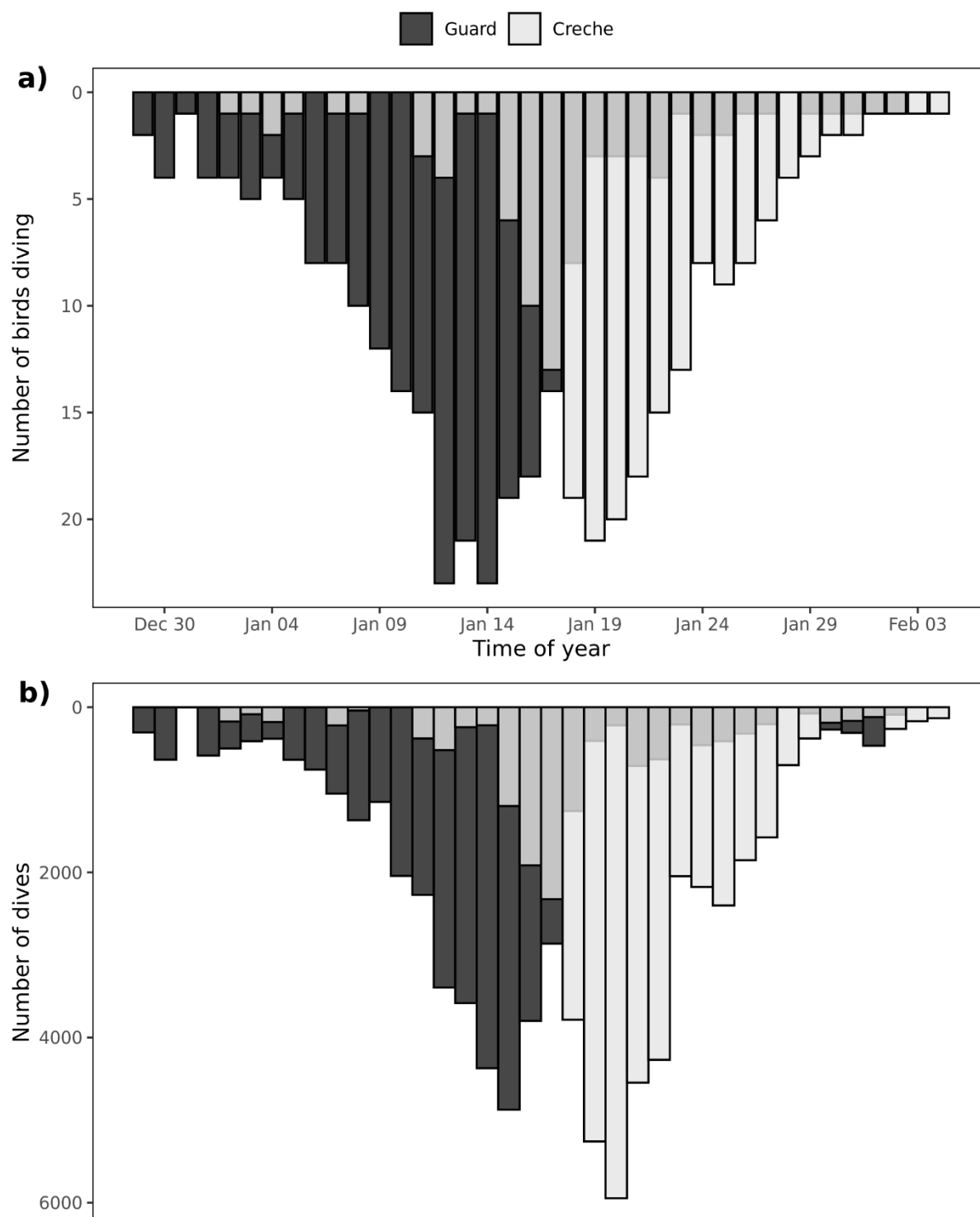
| Response variable            | Predictor variable                 | Coefficients |      |                 |                 |
|------------------------------|------------------------------------|--------------|------|-----------------|-----------------|
|                              |                                    | Est          | SE   | <i>t</i> -value | <i>p</i> -value |
| Total number of bouts        | Intercept                          | 2.97         | 0.16 | 18.54           | <0.0001         |
|                              | Sex (male)                         | -0.49        | 0.21 | -2.28           | 0.26            |
|                              | <b>Stage (crèche)</b>              | 0.44         | 0.26 | 1.66            | <0.0001         |
|                              | <b>Sex (male) * Stage (crèche)</b> | 0.89         | 0.35 | 2.52            | <0.05           |
| Dives per bout               | Intercept                          | 2.47         | 0.10 | 24.26           | <0.001          |
|                              | Sex (male)                         | -0.02        | 0.10 | -0.24           | 0.51            |
|                              | Stage (crèche)                     | 0.15         | 0.07 | 2.16            | 0.06            |
|                              | Sex (male) * Stage (crèche)        | -0.11        | 0.11 | -1.07           | 0.28            |
| Proportion of dives in bouts | Intercept                          | 0.69         | 0.18 | 3.81            | <0.0001         |
|                              | Sex (male)                         | 0.43         | 0.17 | 2.45            | 0.19            |
|                              | Stage (crèche)                     | 0.52         | 0.21 | 2.44            | 0.55            |
|                              | <b>Sex (male) * Stage (crèche)</b> | -0.77        | 0.28 | -2.74           | <0.01           |

4

1 Table S4. Results of linear mixed effects models for dive-level parameters in relation to other dive-  
2 level variables, sex, stage and solar position. Estimated means  $\pm$  SE are presented on the natural log  
3 scale. Results presented as in Table S2.

| Response variable   | Predictor variable                 | Coefficients |      |         |         |
|---------------------|------------------------------------|--------------|------|---------|---------|
|                     |                                    | Est          | SE   | t-value | p-value |
| Depth (m)           | Intercept                          | 3.23         | 0.09 | 34.32   | <0.0001 |
|                     | Sex (male)                         | 0.10         | 0.06 | 1.64    | 0.43    |
|                     | <b>Stage (crèche)</b>              | 0.01         | 0.01 | 0.31    | <0.0001 |
|                     | <b>Sex (male) * Stage (crèche)</b> | -0.14        | 0.02 | -8.10   | <0.0001 |
|                     | Solar                              | -0.01        | 0.01 | -10.45  | 0.16    |
|                     | <b>Solar (quadratic)</b>           | 0.01         | 0.01 | 10.43   | <0.0001 |
| Duration (s)        | Intercept                          | 2.90         | 0.02 | 177.60  | <0.0001 |
|                     | <b>Depth</b>                       | 0.47         | 0.01 | 508.46  | <0.0001 |
|                     | Sex (male)                         | 0.03         | 0.02 | 1.77    | 0.89    |
|                     | <b>Stage (crèche)</b>              | 0.05         | 0.01 | 15.04   | <0.001  |
|                     | <b>Sex (male) * Stage (crèche)</b> | -0.08        | 0.01 | -16.93  | <0.0001 |
|                     | <b>Solar</b>                       | -0.01        | 0.01 | -3.77   | <0.0001 |
|                     | Solar (quadratic)                  | -0.01        | 0.01 | -1.02   | 0.38    |
| Bottom duration (s) | Intercept                          | -0.85        | 0.03 | -24.79  | <0.0001 |
|                     | <b>Depth</b>                       | -0.60        | 0.01 | -218.73 | <0.0001 |
|                     | <b>Duration</b>                    | 1.46         | 0.01 | 289.67  | <0.0001 |
|                     | Sex (male)                         | 0.05         | 0.03 | 2.11    | 0.08    |
|                     | Stage (crèche)                     | -0.01        | 0.01 | 2.38    | 0.78    |
|                     | <b>Sex (male) * Stage (crèche)</b> | -0.19        | 0.01 | -2.82   | <0.01   |
|                     | <b>Solar</b>                       | 0.01         | 0.01 | 2.16    | <0.0001 |
|                     | <b>Solar (quadratic)</b>           | -0.01        | 0.01 | -3.62   | <0.001  |
| Wiggles             | Intercept                          | -0.77        | 0.11 | -6.98   | <0.0001 |
|                     | <b>Bottom duration</b>             | 0.68         | 0.01 | 161.55  | <0.0001 |
|                     | Sex (male)                         | -0.02        | 0.04 | 0.54    | 0.48    |
|                     | <b>Stage (crèche)</b>              | -0.04        | 0.01 | -4.80   | <0.001  |
|                     | Sex (male) * Stage (crèche)        | 0.01         | 0.01 | 1.27    | 0.21    |
|                     | <b>Solar</b>                       | 0.01         | 0.01 | 0.83    | <0.0001 |
|                     | Solar (quadratic)                  | 0.01         | 0.01 | 0.75    | 0.47    |
| ACPUE <sub>d</sub>  | Intercept                          | -1.80        | 0.11 | -15.73  | <0.0001 |
|                     | <b>Duration</b>                    | -0.06        | 0.01 | -14.57  | <0.0001 |
|                     | Sex (male)                         | -0.01        | 0.04 | -0.37   | 0.77    |
|                     | <b>Stage (crèche)</b>              | -0.07        | 0.01 | -7.88   | <0.0001 |
|                     | <b>Sex (male) * Stage (crèche)</b> | 0.07         | 0.01 | 5.41    | <0.001  |
|                     | <b>Solar</b>                       | 0.01         | 0.01 | 1.60    | <0.0001 |
|                     | Solar (quadratic)                  | -0.01        | 0.01 | 0.77    | 0.50    |

1



2

3 Fig. S1. Compiled TDR data showing the available observations of diving activity through time (total n  
 4 = 64 birds, n = 84,521 foraging dives). Displayed over the chick-rearing period are the number of  
 5 recorded a) penguins in the water diving, and b) foraging dives aggregated across all penguins. Shading  
 6 represents guard (black) and crèche (grey) stages, with transparency to show overlap.

7



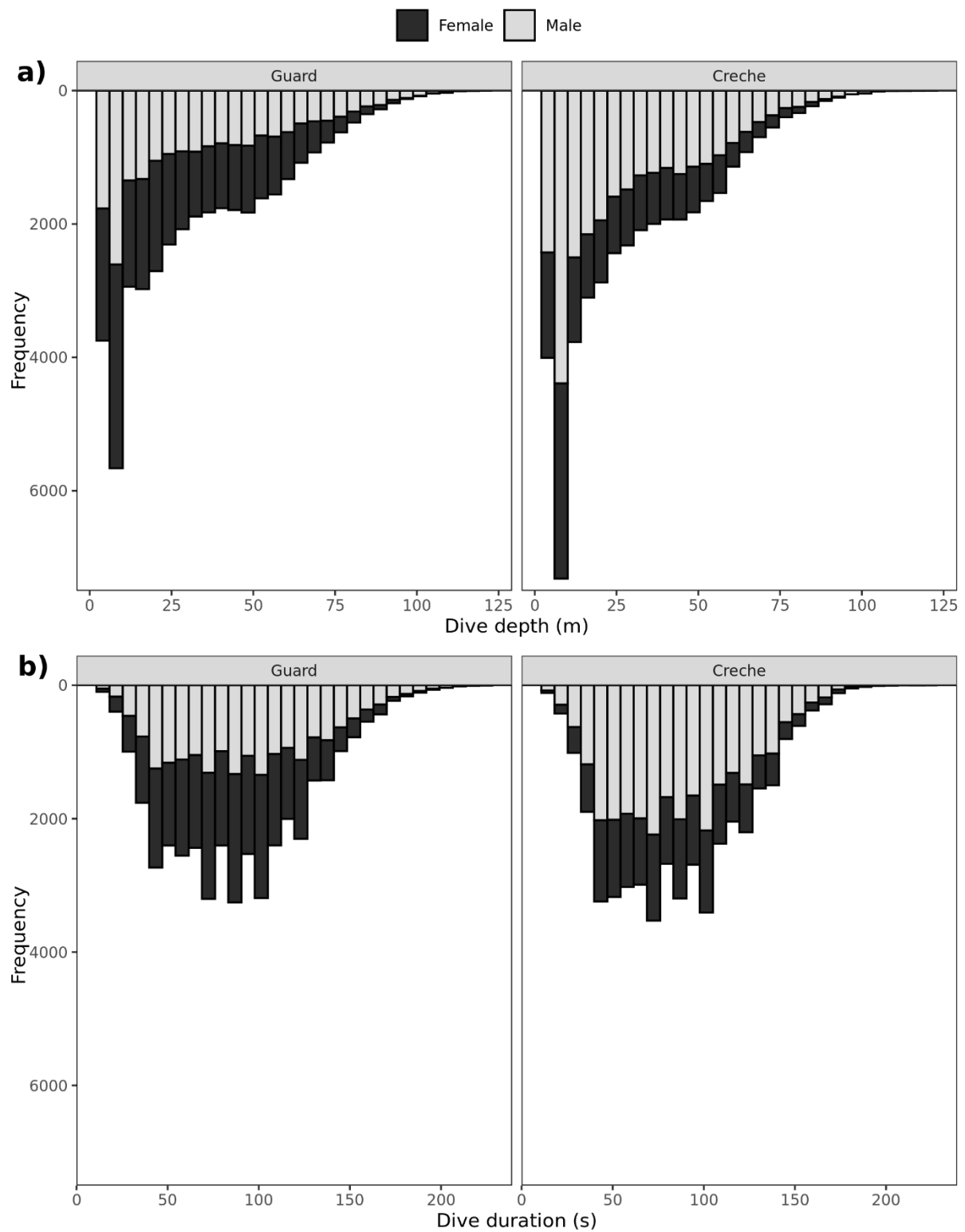


Fig. S2. Compiled TDR data showing the available observations of diving behaviour through time (total  $n = 64$  birds,  $n = 84,521$  foraging dives). Displayed is the frequency of diving a) depth and b) duration for females (black) and males (grey) over the two chick-rearing stages (guard and crèche).