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The occurrence of hypothermia in nestlings of the European Storm-petrel *Hydrobates pelagicus*

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Although Procellariiform nestlings develop independent endothermic thermoregulation at an early age (Wheelwright & Boersma 1979; Ricklefs *et al*. 1980), they may not be able to meet the high energetic costs of maintaining a constant high body temperature during prolonged periods of fasting or cold exposure (Geiser 2008). The ability to reduce body temperature and enter torpor could therefore represent an important survival strategy in the Procellariiformes. Torpor constitutes a facultative hypothermic response, characterised by a regulated reduction in metabolic rate and body temperature, which reduces energy expenditure and potentially facilitates survival under energetically-challenging conditions (McKechnie & Lovegrove 2002; Geiser 2008). This is distinct from an unregulated drop in body temperature that may be the result of an unavoidable pathological response. It is widely acknowledged that Procellariiform chicks have the ability to reduce their energy requirements and enter a state of torpor, yet there are few (mainly brief) documented observations of hypothermia in Procellariiform young (Davis 1957; Scott 1970; Wheelwright & Boersma 1979; Pettit *et al*. 1982; Lockley 1983; Simons & Whittow 1984; Boersma 1986), while some authors have found little or no evidence for hypothermic responses (Bech *et al*. 1991; Gębczyński 1995; Weathers *et al*. 2000).

Here, I describe incidental observations of hypothermia in nestlings of the European Storm-petrel *Hydrobates pelagicus* (hereafter 'Storm-petrel'), recorded while undertaking research at the UK's largest colony at Mousa, Shetland (60°00'N 01°11'W). Hypothermia in the Storm-petrel has previously been reported in young unattended chicks and in older chicks during periods of food deprivation; although Davis (1957), during three years of study, only observed a single 'torpid' chick, Scott (1970) provided greater detail, including measurements of body temperature, of five 'semi-torpid' chicks. Although I did not measure body temperature, the behavioural observations described here provide further evidence of the occurrence and nature of hypothermia in developing Procellariiform chicks.

In the breeding seasons of 2010 and 2011, 75 and 82 occupied Storm-petrel nests, respectively, were monitored from laying through to late postnatal development. In 2011, eight nestlings were found exhibiting behaviours consistent with hypothermia, whereas no such observations had been made in the previous year. In each instance, an unbrooded chick was observed in the nest cavity, displaying no obvious signs of life. On removal from the nest, the only initial indication that a nestling might still be alive was that the downy plumage was dry; otherwise, chicks appeared limp and lifeless with the eyes closed. Following about a minute of being held in the palm of the hand, perceptible signs of life began to appear. Minor movements were initiated, usually starting with the legs, then the head and gaping of the mouth, before a definite heartbeat became detectible, both visually and to the touch. None of the nestlings started calling or regained activity levels typical of healthy chicks, though they may have done so if they had been handled, and thus warmed, for longer. The time during which nestlings were handled and kept outside of the nest was kept to a minimum to minimise investigator effects.

Presumably these nestlings were experiencing large reductions in body temperature, resulting in behaviours characteristic of hypothermia. Drops in body temperature of more than 10°C below the mean were reported, in association with similar behaviours to those described here, in chicks of the European Storm-petrel (Scott 1970) and Fork-tailed Storm-petrel *Oceanodroma furcata* (Boersma 1986). Four of the Storm-petrel nestlings in this study (denoted A–D; see Table 1) were aged between two and five days old when found in a hypothermic state and were unlikely to be capable of independent thermoregulation. Being a facultative hypothermic response, the ability to display torpor is concomitant with endothermic thermoregulation. In 2010, nestlings were brooded for an average (median) of seven days (range 4–11 days) after hatching; this is similar to that reported in other studies (Davis 1957; Mínguez & Oro 2003) and probably coincident with complete development of endothermy. The brooding period was significantly shorter in 2011 (median 6 days, range 3–8 days, Wilcoxon rank-sum: $W = 730$, $P < 0.001$) and it was not uncommon to observe chicks alone in the nest within the first few days after hatching. Hypothermia exhibited by these very young chicks was likely the result of an unavoidable pathological response, as opposed to regulated torpor, associated with the premature cessation of brooding. Indeed, all of these chicks died within three days of entering hypothermia.

The other four hypothermic nestlings (denoted E–H; see Table 1) ranged in age from six to 20 days old and presumably were all competent of endothermic thermoregulation. Only two of these nestlings (F & H) showed signs of recovery from their hypothermic state, presumably associated with a rise in body temperature back towards normothermia, while the other two chicks (E & G) were found dead the following day. I refer to recovery as a gain in mass and regain of normal lively behaviour, irrespective of subsequent successful fledging. The two former nestlings were found to have regained a normal lively state, following receipt of food, as evidenced by increases in mass of 4.6 g and 7.7 g within 24 hours and 96 hours respectively (all mass measurements were adjusted to a standardised time to account for mass loss during the day between feeds, according to Bolton (1995)). Parental

Table 1. Details of eight European Storm-petrel *Hydrobates pelagicus* nestlings (denoted by the letters A–H) observed exhibiting hypothermic responses. Data presented include age at which first unattended, age when first observed in hypothermic state, days elapsed between first record of hypothermia (H) and recovery (R) or death (D), mass at hypothermia (H) and recovery (R), and fledging success. The table is divided into those nestlings presumed to be incompetent and competent of endothermic regulation at the onset of hypothermia and thus incapable and capable of displaying torpor, respectively.

Nestling ID	Age unattended (days)	Age (days)	Days elapsed (H–R or H–D)	$Mass^H$ (g)	$Mass^R$ (g)	Fledged
Presumed incompetent of endothermic regulation						
A	2	2	1^D	4.9	NA	No
B	3	3	1^D	5.3	NA	No
C	3	4	1^R, 3^D	5.4	8.1	No
D	5	5	1^D	5.9	NA	No
Presumed competent of endothermic regulation						
E	6	6	1^D	9.0	NA	No
F	6	10	1^R	7.1	11.7	Yes
G	5	11	1^D	10.4	NA	No
H	7	20	4^R	17.4	25.1	Yes

Figure 1. European Storm-petrel *Hydrobates pelagicus* chick, seven days old and capable of endothermic thermoregulation. 1 September 2010, Mousa, Shetland. © *Hannah Watson*.

brooding of these chicks had ceased and they had already been unattended for four and 13 days, respectively, prior to becoming hypothermic. These two instances of hypothermia may represent examples of genuine torpor - an adaptive and facultative response to an energetic challenge, presumably due to exposure to a long period of cold or starvation. While a third nestling (C) did show signs of recovery within 24 hours, it was found dead a further two days later; at just four days old, the nestling was unlikely to have fully developed endothermy and thus the hypothermic response observed may not have represented actual torpor. This chick was in fact accompanied in the nest by an adult when observed in a hypothermic state, but was not being actively brooded.

The onset of torpor in birds has been linked to a shortage of food (Koskimies 1948; Prinzinger & Siedle 1988) and body temperature was found to be strongly correlated with food load in the Fork-tailed Storm-petrel (Boersma 1986). Disruptions in provisioning causing prolonged starvation could thus trigger entry into a facultative hypothermic state. Scott (1970) noted a marked reduction in feeding frequency by European Storm-petrels when the wind was Beaufort Force 7 (> 14 m/s) or greater, while Davis (1957) found evidence for a reduction in meal size under such rough conditions, though neither author linked weather conditions with observations of hypothermia. In the first 16 days of August 2011, during which six instances of hypothermia were recorded, the average daily wind speed at Mousa (recorded from the nearest station located at Lerwick, c. 33 km away) was significantly higher (median 6.2 m/s, range 3.1–10.8 m/s) than in 2010 (median 4.6 m/s, range 2.1–6.2 m/s, Wilcoxon rank-sum: W = 46.5, P = 0.006), when no hypothermic chicks were observed. On seven out of those 16 days, the average wind speed was equal to or greater than 7.2 m/s (max. 10.8 m/s) in 2011, while it never exceeded 6.2 m/s during the same period in the previous season. While these daily mean wind speeds do not approach the speeds referred to by Scott (1970) and Davis (1957), the differences observed may still be sufficient to affect provisioning rates; data on maximum wind speed are not known. Mean ambient temperatures were not significantly different during the same period in 2011 (median 12.5 °C, range 10.3–15 °C), compared with 2010 (median 12.7 °C, range 11.8–14.5 °C, Wilcoxon rank-sum: W = 145, P = 0.184), suggesting that the occurrence of hypothermia in 2011 was not driven by prolonged exposure to low temperatures.

Although I did not observe provisioning behaviour, it seems highly likely that the occurrence of temporary hypothermia was the result of indirect effects of strong winds resulting in reduced feeding frequency and/or food load. Nestling survival was significantly lower in 2011 (37.8%) compared with 2010 (57.3%, GLMM: z = -2.53, P = 0.011), a further indication of less favourable conditions for successful chick-rearing. Regardless of whether the hypothermic responses described are facultative (i.e. genuine torpor) or not, the observations indicate that the body temperature of developing Storm-petrels can be highly plastic, even once endothermic thermoregulation has fully developed. The ability to survive periods of hypothermia may be adaptive, facilitating survival under less favourable conditions, though it may also constrain growth (Boersma 1986) and delay fledging date (Davis 1957). The observations documented here offer further insight into the nature and occurrence of torpor in Procellariiformes, but more detailed studies, particularly the recording of body temperature over time, are required to improve our understanding of the ability to display a regulated hypothermic response and the consequences for individual growth and development.

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