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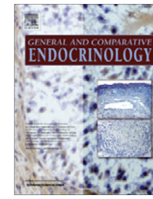

Corticosterone and migratory fueling in Northern wheatears facing different barrier crossings

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ABSTRACT

Corticosterone, at baseline and moderately elevated levels, is thought to regulate energy mobilization during the predictable life-history cycle. In birds, corticosterone is known to be moderately elevated during migration, and some experiments on captive, but migratory active birds have shown that exogenous corticosterone can positively affect food intake and fat deposition, i.e. fueling. We present observations which indicate that in wild birds endogenous corticosterone does not promote refueling during migratory stopovers. We took a comparative approach and studied two subspecies of Northern wheatears (*Oenanthe oenanthe*) during their simultaneous spring stopovers on Helgoland, a small island some 50 km off the German coast. In spring *O. oenanthe* have to travel relatively short distances from Helgoland to their next stopover or breeding sites, whereas *Oenanthe leucorhoa* face a lengthy overseas journey. Consequently, for their next flight bout *leucorhoa* wheatears deposit more fuel, more rapidly than *oenanthe* wheatears. Corticosterone levels, however, were lower in *leucorhoa* than *oenanthe* wheatears, contradicting the idea that corticosterone promotes migratory refueling. This finding was solidified by the observation that actual fuel deposition rate was negatively correlated with corticosterone level. We also observed a positive correlation between corticosterone level and fuel stores. Together these findings suggest that, rather than promoting migratory refueling, corticosterone may function as a readiness cue, with levels increasing towards departure from the stopover site.

1. Introduction

For migratory birds, early arrival at the breeding site has been shown to positively affect breeding success e.g. (Currie et al., 2000; Smith and Moore, 2005). In between flight bouts, most migratory birds make one or more stopovers during which they replenish their fat and protein loads. Because the time spent refueling at stopover sites by far exceeds the time in actual flight (Green et al., 2002; Hedenström, 1997), rapid refueling may advance the arrival at the breeding site. The rate of refueling, termed fuel deposition rate, has been shown to depend on environmental factors such as food availability (Schaub and Jenni, 2000), weather (Jenni and Schaub, 2003; Schmaljohann and Dierschke, 2005), and predation pressure (Schmaljohann and Dierschke, 2005), as well as intrinsic factors such as molt (Fransson, 1998; Schaub and Jenni, 2000) and body mass (Kuenzi and Moore, 1991; Schaub and Jenni, 2001). Also, several experiments with captive, but migratory active birds suggest that corticosterone, the main glucocorticoid hormone in birds, may play a role in migratory (re)fueling. Corticosterone, at baseline and moderately elevated levels, is thought to have a permissive effect on food intake, and may affect energy mobilization during the predictable life-history stages (Dierschke and Delingat, 2001, and references therein). Corticosterone levels increased significantly in dark-eyed juncos (*Junco hyemalis*) after these were photostimulated into migratory condition (Holberton et al., 2008) and pharmacological blocking of this increase inhibited mass gain (Holberton et al., 2007). Similarly, in white-crowned sparrows (*Zonotrichia leucophrys gambelli*) blocking of the low-affinity glucocorticoid receptor (GR) suppressed food intake (Landys et al., 2004). Red-eyed vireos (*Vireo olivaceus*) captured from a stopover site, caged for several weeks, and subsequently fed corticosterone filled mealworms had a greater feeding rate than did control caged birds (Lõhmus et al., 2006). Finally, in white-throated sparrows (*Zonotrichia albicollis*) long-term administration of exogenous corticosterone resulted in increased body mass through increased fat deposition (Long, 2007). These experiments show that exogenous corticosterone can affect food intake and even fattening, and suggest that its role in migratory fueling is more than merely permissive. However, whether endogenous corticosterone actually facilitates migratory (re)fueling in wild birds is at present unresolved. In several species corticosterone levels are moderately elevated during spring, but not fall migration e.g. (Holberton, 1999; Piersma et al., 2000; Romero et al., 1997), and in refueling European robins (*Erithacus rubecula*) levels increased with the pro-

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gress of the migratory season (Falsone et al., 2009). Possibly, in the robins, the moderately elevated corticosterone levels promote an increased foraging activity and increased fuel deposition rate in late-migrating birds (Falsone et al., 2009). However, in bar-tailed godwits (*Limosa lapponica*) corticosterone levels drop after arrival at stopover sites, remain low during refueling and rise just prior to departure (Landys-Cianelli et al., 2002).

If corticosterone indeed promotes refueling during stopover, levels should be adjusted to the future energetic requirements of individual birds. For example, for birds that need to deposit fuel, this need will be higher for individuals that have to cross a large barrier to reach their next stopover or breeding site than for individuals that do not face such a barrier. Consequently, corticosterone levels may need to be higher in the former than in the latter individuals. Whether or not corticosterone levels are actually adjusted to match expected energetic demands of the next flight bout is currently unknown. One of the reasons for this is that, within a species, the destination (next stopover or breeding site) of individual birds is usually unknown. The long-distance migrating Northern wheatear (*Oenanthe oenanthe*) provides an exception to this in the form of two subspecies that have different migratory destinations, but that make simultaneous spring stopovers on Helgoland, a German offshore island. The subspecies *O. oenanthe* breeds throughout Northern and central Europe, North Asia–Eastern Siberia, and the Northwestern parts of North America (Del Hoyo et al., 2005). *O. leucorhoa* breed in Iceland, Greenland, the Faroe Islands, and Northeastern Canada (Del Hoyo et al., 2005). This means that in spring *O. oenanthe* have to travel relatively short distances from Helgoland to their next possible stopover or breeding sites, with sea crossings ranging ca. 50–500 km (Dierschke and Delingat, 2001; Dierschke and Delingat, 2003). *O. leucorhoa*, on the other hand, face a much longer overseas journey (ca. 1000–2500 km) to reach their next stopover or breeding sites from Helgoland (Delingat et al., 2011; Dierschke and Delingat, 2001; Dierschke and Delingat, 2003). It should be noted though that, when weather conditions are unfavorable, some *leucorhoa* wheatears avoid a direct sea crossing and detour through mainland Europe (Haftorn, 1971; Schmaljohann and Naef-Daenzer, 2011). Nevertheless, on Helgoland, *leucorhoa* wheatears make longer spring stopovers during which they deposit more fuel than *oenanthe* wheatears (Delingat et al., 2006; Dierschke and Delingat, 2001; Dierschke et al., 2005). Importantly, daily fuel deposition rates are also higher in *leucorhoa* than *oenanthe* wheatears, which appears to result from a combination of higher food intake rate and a more efficient assimilation of food (Dierschke et al., 2005, Schmaljohann et al. in prep). These observations on refueling indicate that the two subspecies accurately anticipate the different energetic demands of their respective next flight bouts, which renders this system highly suitable for comparative field endocrinology.

The objective of the current study was to determine if corticosterone promotes refueling during stopover. For this purpose, we determined corticosterone levels in both *O. oenanthe* and *O. leucorhoa* during their simultaneous spring stopovers on Helgoland. Additionally, we re-trapped birds to calculate their rate of refueling. If corticosterone promotes refueling we expected that (a) accounting for fuel loads, *leucorhoa* wheatears have higher corticosterone levels than *oenanthe* wheatears, and (b) fuel deposition rate is positively correlated with corticosterone level.

2. Methods

2.1. Study site and field methods

Northern wheatears are small (ca. 25 g) insectivorous nocturnal long-distance migrants. Data were collected on Helgoland (54°11′N, 07°55′E), a small (1 km^2) island ca. 50 km off the German North Sea coastline. In 2012, during the peak of spring migration (mid April–late May), Northern wheatears were caught using mealworm-baited spring traps. All birds were trapped between 8 am and 7 pm, well after sunrise and well before sunset. Traps were monitored continuously and when a bird was caught it was taken from the trap and blood-sampled (ca. 100 μl) immediately from the wing vein. The time from closing of the trap until the end of blood-sampling was recorded and will be referred to as 'sampling time' in the remainder of the text. The plasma was separated within 5 h of capture and frozen at −20 °C until hormone assaying. Birds were sexed (on plumage), ringed, and fitted with a unique combination of three color-rings for later identification in the field. Body mass was measured to the nearest 0.1 g using an electronic balance and fat stores were scored according to (Kaiser, 1993) on a scale ranging from 0 (no fat) to 8 (furcula and abdomen bulging, and breast covered with fat). Wing length (maximum chord) was used to separate the subspecies; males and females with wing length exceeding 102 and 97 mm, respectively, were treated as belonging to the *leucorhoa* subspecies, and males and females with wing length below 99 and 96 mm, respectively, were treated as belonging to the *oenanthe* subspecies (Svensson, 1992). Birds that could not be assigned to subspecies on wing length were not considered in this study. Each day the number of wheatears present on the island was estimated using data on the location, time, sex and color-ring combination (if any) of all wheatears seen by us on the island that day. Northern wheatears do not breed on Helgoland. All procedures were approved by the Ministry for Agriculture, the Environment and rural Areas, Schleswig–Holstein, Germany.

2.2. Fuel load and fuel deposition rate

Each bird's fuel load was calculated as: fuel load = (body mass [g]−lean body mass [g])/lean body mass [g]. Lean body mass was calculated after (Schmaljohann and Naef-Daenzer, 2011). There was a strong positive correlation between calculated fuel loads and the visual scores of fat stores (Spearman's rho = 0.7, $p < 0.001$, $n = 109$), but since fuel load provides a more objective estimate of fuel stores than visual scoring of fat, we used the former in all analyses.

To calculate fuel deposition rates, individuals have to be weighed at two or more separate occasions. For this purpose two electronic balances baited with mealworms (in a bowl) were placed in the trapping area during the late afternoon. A video recorder was positioned 2 m away from a balance in such a way that both the display and a visiting bird's color-rings could be seen simultaneously. Seven birds that we had previously trapped, weighed and color-ringed visited the balances at least once. On these occasions the display was read immediately before the bird hopped on the balance and immediately after that when the bird was perched on the bowl with mealworms. A bird's mass was calculated by subtracting the former from the latter. To exclude immediate mass gains resulting from ingestion of mealworms, for each bird we always used the day's first re-weighing. Next to the seven "remote re-weighted birds", five birds could be re-weighed because they were re-trapped. Because in northern wheatears on Helgoland the rate of refueling is not linear over the day, but generally is highest in the morning (Delingat et al., 2009), fuel deposition rates are ideally calculated over a period approximating 24 h. Such ideal data were available for 8 of the12 re-weighed birds. For these birds, fuel deposition rate was calculated as body mass gain (or loss) within 24 ± 1hrs or a multiple of 24 ± 1 h divided by lean body mass and the number of 24 h periods between the measurements (Delingat et al., 2006). The remaining four birds were trapped and weighed for the first time in the