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Adaptive management of body mass by Siberian jays

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A profusion of theoretical and empirical studies has successfully explored the issue of adaptive management of body mass by small birds threatened with both starvation and predation. In addition to diurnal body mass cycles, body mass tends to increase with either poorer mean conditions or more variable conditions, such as those often experienced during winter. In many species, individual dominance status will affect access to food and predation risk, and is therefore predicted to influence patterns of optimal body mass further. We investigated body mass regulation via repeated measurements without capture in groups of Siberian jays, *Perisoreus infaustus*, during autumn. As predicted, body mass of individuals increased throughout the day and towards the winter and was higher during colder periods. Jay body mass was also correlated with wind chill conditions 23 h before. This makes sense since conditions 24 h earlier were a better predictor of current conditions than conditions either 12 or 48 h earlier. Dominant birds (i.e. breeders) that were large carried relatively lower fat reserves than large subordinate individuals. The opposite was true for morphologically small birds. Together this suggests tighter requirements for individual variation in mass for dominant breeders in these groups. Our findings in this food-hoarding corvid are in general agreement with models and results concerning much smaller birds.

Within-individual variation in body mass of small birds is largely due to adaptive regulation of fat reserves through behaviour rather than the result of constrained responses to food limitation (e.g. Thomas 2000; Lilliendahl 2002; Macleod et al. 2005a, b; Brodin 2007). This is supported by experimental studies showing that birds reach the same body mass at dusk regardless of their body mass at dawn (Lilliendahl et al. 1996; Thomas 2000). This suggests that there are costs to increased body mass in addition to the obvious benefits. Such costs may include mass-dependent predation risk, flight costs and metabolic rates (Witter & Cuthill 1993). As the relative costs and benefits of body reserves can vary, optimal mass differs within and between individuals.

Because reserves can buffer against energetic shortfalls, increases in body mass are expected in response to decreased temperature and food availability and to increased variation in these two factors as well (Brodin 2007; Dall 2010). Empirical studies have shown that increases in body mass are correlated with decreased food abundance or decreased ambient temperatures, with low overnight temperatures, either during the current period or in the period directly preceding it being especially influential (Haftorn 1976; Waite 1992; Witter et al. 1995; Gosler 1996; Macleod et al. 2005a; Krams et al. 2010). Experimental studies that have manipulated predictability of food supply in captive birds do not always support the prediction of increased body mass (Witter et al. 1995; Acquarone et al. 2002; Cucco et al. 2002; but see Cuthill et al. 2000), although hoard size has been observed to be increased under more variable food supply (Hurly 1992). In other areas of foraging behaviour, experiments on wild birds have proven important to understand the responses seen in captivity (Ratikainen et al. 2010). Therefore, experiments carried out in the environments in which these mass regulation strategies evolved are needed to resolve whether and how predictability of food supply affects energetic reserves.

Various social or ecological factors may affect both individual mean access to, and predictability of, food supplies in addition to individual predation risk. It is therefore expected that subordinates with lower and less predictable access to food and perhaps also a different predation risk while foraging will have larger reserves (Brodin & Clark 2007). However, empirical studies on this topic provide contrasting results (Ekman & Lilliendahl 1993; Gosler 1996; Pravosudov & Lucas 2000; Polo & Bautista 2002; Krams et al. 2010). Caching has also been predicted to decrease the effect of resource unpredictability (McNamara et al. 1990), but again this has not always been confirmed in empirical studies (Pravosudov & Grubb 1997, 1998). It has also been predicted that hoarding birds should respond to greater variability by increasing their hoards rather than

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body mass, and an experiment with marsh tits, *Poecile palustris*, has confirmed this (Hurly 1992).

In the northern boreal forests there are large differences in temperature and length of daylight between the different seasons. Seasonal changes in body mass can vary within and between species, but generally an increase in body mass before winter has been observed in many studies (Haftorn 1976; Smith & Metcalfe 1997; Macleod et al. 2005a; but see Cooper 2007). The seasonal increase in body mass can be attributed to longer nights and lower temperatures during winter putting a larger demand on evening reserves. The constant dawn mass theory predicts that only evening mass is increased compared to summer, while true winter fattening is only apparent when body mass is higher in both the morning and the evening during winter compared to summer (Lehikoinen 1987). Such true winter fattening is only expected if winter, in addition to being on average more energetically demanding, is a less predictable period. For example, winter can be less predictable owing to more variable temperatures requiring greater reserves to ensure overnight survival. Lower predictability can also be caused by more variable weather leading to more frequent interruptions in foraging.

A daily increase in body mass has been observed in many studies (e.g. Haftorn 1976; Macleod et al. 2005b; Cooper 2007). The timing of daily body mass increase varies between species and between individuals within species. Theoretical developments show that unpredictability in access to (in combination with scarcity of) food should lead to earlier and larger mass gain before night (Bednekoff & Houston 1994), and this has generally been confirmed by empirical studies (Pravosudov & Grubb 1997; Polo & Bautista 2006). Other factors such as food hoarding and predation may also interact with climatic conditions in their effect on the diurnal body mass patterns. As a result, a range of different curvilinear diurnal mass gain trajectories can be predicted, including simple linear increases (Brodin 2000).

We investigated the daily and seasonal variation in body mass of wild Siberian jays, *Perisoreus infaustus*, in response to variation in temperature. In addition, we examined differences in body mass between individuals of different social status and of variable body size. Siberian jays (approximately 85 g) are considerably larger than the bird species of 10–20 g that are traditionally considered 'small' in this field (Brodin 2007). This is especially interesting given the number of existing studies concerning body mass regulation in small birds, which may be thought to respond more to external factors because they have a more limited energy budget than larger bird species. As a result, relatively little is known about body mass regulation in larger birds and this brings into question the generality of the earlier findings. The current study was carried out during autumn when weather conditions are less adverse and temperatures are usually positive and less variable during the daytime. However, the birds were working hard to build up food caches for the coming winter. Jays are adapted to long, cold winters with temperatures regularly going below −20 °C, and our study also extended into early winter when the first snowfall can be expected. We therefore expected to see the same patterns in body mass that reflect the more extreme responses expected during winter itself. Although previous theoretical and empirical research has focused on the most energetically challenging winter periods, we might expect to see the same patterns of body mass adjustments as the environment becomes more challenging during the autumn. Many mass-dependent costs and benefits, such as predation risk, are also likely to be just as important for the jays during this period of food collection and hoarding, because they have to venture much more into open foraging areas than in the winter. Before winter we therefore expect to see true winter fattening and the same adaptive responses in body mass to natural variation in weather conditions.

Importantly, this study includes many measurements of the same individuals in the wild and can therefore address issues concerning within-individual regulation of body mass. Previous studies have tended to include either repeated measurements of body mass of a few captive individuals (Waite 1992; Lilliendahl et al. 1996; Pravosudov & Grubb 1997; Cuthill et al. 2000; Lilliendahl 2000) or many measurements of different individuals that were captured in the wild (Haftorn 1976; Gosler et al. 1995; Gosler 1996; Smith & Metcalfe 1997; Macleod et al. 2005a); very few examples of repeated measurements of the same individuals in the wild exist (e.g. Macleod et al. 2005b). The repeated measures of wild individuals is important because the relationships between body mass and any explanatory variables may not be the same as any between-individual relationships; it is therefore not always appropriate to investigate individual body mass regulation from studies of between-individual differences (Witter & Cuthill 1993). Another advantage of our data is the fact that the birds were not captured to obtain the measurements. Therefore birds were not stressed during repeated captures, and no effects of stress or distortions of the daily cycle on body mass are expected.

METHODS

Study Population and Data Collection Methods

The Siberian jay is a medium-sized passerine, but a relatively small corvid, living in Eurasian boreal taiga forests. It is a highly territorial, group-living bird. Group size may range from two to seven; groups consist of a breeding pair and may also include their retained offspring from earlier years and immigrants from other territories (Ekman et al. 1994, 1999). Siberian jays are omnivores that eat fungi, berries, seeds, invertebrates, small mammals and carrion (Andreev 1978; Borgos & Hogstad 2001). They are long-term food hoarders, and throughout the autumn they gather food and store individual items for the winter. In most cases, these food caches are retrieved by the same individual that stored them (Ekman et al. 1996). Winter conditions can be very harsh owing to low temperatures and snow cover concealing possible food sources on the ground. Despite the severe conditions, the jays stay in their territories year round.

Our study population is resident in forests close to Arvidsjaur in northern Sweden (65°40′N, 19°0′E). This study population is part of an ongoing study by researchers from Uppsala University, and all individual Siberian jays are ringed with a unique combination of colour rings, measured (i.e. tarsus), sexed and their status (as breeder, offspring or immigrant) is determined as part of this study (Ekman et al. 1994, 2000, 2002). Siberian jays are usually not afraid of humans and can thus be easily observed without disturbance effects. The population used in this study has also been habituated to humans over many years using occasional supplementary food. A total of 45 individuals in 13 groups were included in this study. Eight additional individuals, belonging to five of the groups, were weighed but not included in the analyses because their sex or status in the group was not known. Over the course of the study 15 male breeders, 13 female breeders, seven male offspring, three female offspring, four male immigrants and six female immigrants were included in the study. Of these, one offspring and two immigrants from the first year of study were later included as breeders in the same territories in which they had previously been subordinates. The birds included in this study were part of experiments that included supplementary feeding one or two times on most days throughout the study periods, lasting from 1 September until 13 October in 2006, from 12 September until 21 October in 2007 and from 12 September until 25 September in 2008 (Ratikainen et al. 2010, 2012; Ratikainen 2012). All individuals were weighed at the