



Short-term changes in body condition in relation to habitat and rainfall abundance in American redstarts *Setophaga ruticilla* during the non-breeding season

Frédéric Angelier, Christopher M. Tonra, Rebecca L. Holberton and Peter P. Marra

F. Angelier (angelier@cebc.cnrs.fr), Centre d'Etudes Biologiques de Chizé, CNRS, UPR 1934, FR-79360 Villiers en Bois, France. – C. M. Tonra and R.L. Holberton, Lab. Avian Biol., School of Biol. and Ecol., Univ. of Maine, Orono, ME 04469, USA. – P. P. Marra, Smithsonian Migr. Bird Center, National Zool. Park, Washington DC 20008, USA.

In migratory birds, environmental conditions during the stationary period of the non-breeding season are crucial to consider because they ultimately affect the fitness of individuals by influencing their subsequent migration, breeding success and survival. Although a few studies have investigated the influence of non-breeding habitat on the capacity of individuals to cope with long-term seasonal rainfall fluctuations, it remains unknown how habitat quality and variations in rainfall abundance – at a monthly scale – interact to affect non-breeding condition of migrating birds. In this study, we examined the influence of monthly changes in rainfall abundance on body condition of non-breeding female redstarts *Setophaga ruticilla* living either in a high quality habitat (mangrove) or in a low quality habitat (scrub). Body condition of both mangrove and scrub redstarts showed important variations over the study period, demonstrating for the first time that body condition of non-breeding female redstarts can change rapidly in response to short-term fluctuations in rainfall. Importantly, we found that female redstarts living in mangrove were usually in better condition during periods of low rainfall compared to females living in scrub. However, body condition did not differ between mangrove females and scrub females during an episode of frequent, heavy precipitation. Importantly, our study also demonstrated that the duration of a perturbation is an important determinant of body condition in redstarts since a prolonged drought resulted in similar low body condition for birds from both habitats. Age was not correlated with body condition whatever the habitat and the rainfall conditions. Our results demonstrate that high quality habitat can temporarily reduce the deleterious effect of a short-term drought on body condition, but also, that a habitat of low quality does not constrain individuals when climatic conditions are optimal.

In vertebrates, environmental perturbations such as food shortages or harsh weather can have an overall negative effect on breeding success and survival (Coulson et al. 2001, Garel et al. 2004, Altwegg et al. 2006). However, individual responses to deleterious climatic events are complex because populations are heterogeneous and such events do not equally affect all individuals in a population (Beauplet and Guinet 2007, Weladji et al. 2008). This heterogeneity primarily results from two kinds of factors. First, intrinsic variables such as age or phenotypic characteristics can determine the extent individuals are vulnerable to deleterious climatic events (Barbraud and Weimerskirch 2005, Angelier et al. 2007a, b, Beauplet and Guinet 2007). For instance, young breeders usually perform less well than older ones under adverse environmental conditions, whereas this difference can be attenuated under good environmental conditions (Coulson et al. 2001, Weladji et al. 2008). Second, extrinsic variables such as habitat quality or population density can affect an individual's response to

additional environmental perturbation through their capacity to modulate perturbation effects on resource availability and individual performance (Zanette et al. 2006, Sperry and Weatherhead 2008). For instance, high-quality habitat is known to attenuate the negative effects of food shortages or harsh weather on the reproductive performance of individual birds (Löhmus 2003, Byholm and Kekkonen 2008).

In birds, environmental conditions during the non-breeding season are crucial to consider because they can ultimately affect the fitness of individuals by influencing their subsequent migration, breeding success, and survival (the concept of 'carry-over effects', Marra et al. 1998, Reudink et al. 2008). To date, several studies have investigated how age and habitat interact to affect individual performance and body condition of migratory birds on the non-breeding grounds (Marra and Holberton 1998, Strong and Sherry 2000, Marra and Holmes 2001, Studds and Marra 2005, 2007, Brown and Sherry 2006, Newton

2006) but only a few of them have examined this interaction in relation to long-term fluctuations in rainfall conditions (i.e. over several months: Marra and Holberton 1998, Marra et al. 1998, Marra and Holmes 2001, i.e. comparisons between years: Studds and Marra 2007). The influence of both age and habitat quality on the capacity of individuals to cope with short-term perturbations – at a monthly scale – has never been studied during the non-breeding period. However, the short-term dynamics of environmental perturbations deserve attention when focusing on carry-over effects because the timing, the duration and the intensity of a non-breeding perturbation is likely to determine its effect on non-breeding season performance and life-history decisions (e.g. survival and timing of migration, reviewed in Newton 2006). For instance, a short-term perturbation can possibly have less adverse effects on individual performance than a prolonged perturbation because individuals can probably deal with the perturbation without entailing important fitness costs during a limited period only (duration of the perturbation). Similarly, on the non-breeding grounds, a late perturbation can lower the pre-migration fattening rates of individual and, thus, delay their migration to the breeding grounds and lower their subsequent reproductive performance whereas an early perturbation may have fewer adverse consequences (timing of the perturbation, Schaub and Jenni 2001, Newton 2006, Gordo 2007, Bauer et al. 2008, Reudink et al. 2009).

In this study, we examine whether age, habitat quality and short-term within season fluctuations in rainfall interact to affect non-breeding individual performance in a migratory bird, the American redstart *Setophaga ruticilla*. In insectivorous birds, rainfall abundance may affect body condition either directly through an effect of drought on body condition or indirectly through an effect on insect abundance and, thus, food acquisition (Strong and Sherry 2000, Studds and Marra 2007, Smith et al. 2010). Here, we investigated the influence of monthly changes in rainfall abundance – the main determinant of food availability during the wintering period (Studds and Marra 2007) – on body condition of female redstarts. We examined this question during a year of overall high rainfall characterized by high monthly variation in rainfall abundance. In birds, body condition can be a major proximate factor influencing carry-over effects (Marra et al. 1998, Studds and Marra 2005) since it is known to determine strategic decisions of an organism (the concept of ‘state-dependent life-history strategies’, McNamara and Houston 1996). Moreover, body condition is known to decrease when individuals cannot acquire enough energy to maintain a balanced energetic budget (‘the nutritional stress hypothesis’, Moe et al. 2002, Trites and Donnelly 2003). On the other hand, body condition can also be adaptively modulated to decrease in response to energetic constraints that helps reduce an individual’s basal energetic needs and energetic costs of locomotion (‘the programmed anorexia hypothesis’, Mrosovsky and Sherry 1980, Moe et al. 2002). Although these hypotheses seem in opposition, both suggest that a decrease in body condition mirrors a constrained energetic situation and body condition is therefore a good indicator of the degree to which non-breeding birds are constrained by their environment (Marra and Holberton 1998, Marra

et al. 1998, Holberton and Able 2000, Brown and Sherry 2006). Following findings from previous studies conducted on this species but over a larger time-frame (Marra and Holberton 1998, Marra and Holmes 2001, Studds and Marra 2007), we made three predictions. First, we predicted that short-term reduction in rainfall will be associated with poor body condition in female redstarts. Second, we predicted that the negative effect of rainfall reduction on body condition will be attenuated in habitats of high quality (black mangrove forests) in comparison to habitats of low quality (second-growth scrub). Finally, consistent with previous findings (Marra et al. 1998, Studds and Marra 2005) we predicted that age will not influence the degree to which redstart body condition is affected by a reduced rainfall abundance.

Methods

Study area and species

Our study was carried out from 25 January to 17 April 2008 at the Font Hill Nature Reserve, 13 km west of Black River, St Elizabeth parish, Jamaica, West Indies. The American redstart is a migratory passerine that breeds throughout North America and overwinters in the Caribbean, Central America, and northern South America. Redstarts begin arriving in Jamaica and establish territories in September and remain on those territories for 6–7 months until they depart on spring migration between late April and mid May. Non-breeding American redstarts are ideal for examining the combined influences of age, habitat and rainfall abundance on body condition for several reasons. First, young (hatch-year; hereafter HY) and older (after hatch-year, hereafter AHY) birds establish their non-breeding territories along a moisture gradient that also corresponds to a habitat quality gradient, a range of which (high quality black mangrove forest to low quality second-growth scrub habitat of low quality) occurs within our study site (see Marra and Holberton 1998, Marra and Holmes 2001 for further details). Second, rainfall abundance is known to dramatically vary within the non-breeding season in Jamaica. The first half of the non-breeding season is characterized by frequent and heavy precipitation (October–December), whereas precipitation is infrequent and unpredictable during the second half (January–March, Marra and Holberton 1998, Studds and Marra 2007). This study was performed in 2008, which was a very wet year in Jamaica (292 mm total from January to March compared to a long-term average of 147 mm). When considering the January–March period, 2008 was the wettest year since 1995 (Studds and Marra 2007). This primarily resulted from abundant rainfall in March (204 mm), but February was also quite wet with 72 mm of rainfall. For context, some years <50 mm of rainfall occurs over the entire January–March period (2002, 2005 and 2007 for example, Studds and Marra 2007). These comparisons emphasize that we examined the influence of fluctuations in rainfall on body condition under overall good environmental conditions.

Study design

A total of 99 female redstarts were sampled during three distinct periods. Each female was sampled only once. These periods were selected according to their specific and different environmental conditions. First, 32 females were captured from 25 January to 25 February when precipitation was low (period A, 71.5 mm of rain, 2.23 mm d⁻¹, Fig. 1). During this period, the scrub habitat was already dry while most areas of mangrove habitat was still under significant amounts of standing water as a result of the heavy precipitation that occurred during the prior wet season between September and January. Second, 35 birds were captured from 5 March to 24 March when precipitation amounts were still low (period B, 22 mm of rain, 1.1 mm d⁻¹, Fig. 1). During this period, the scrub habitat continued to be dry and the water level was decreasing in the mangroves, resulting in the drying of areas bordering the mangroves. Finally, 32 birds were captured from 25 March to 17 April when there was unusually heavy and frequent rainfall (period C, 300.4 mm of rain, 12.52 mm d⁻¹, Fig. 1). During this period, the mangroves were again submerged and the scrub habitat was wet with emergent leaves and flowers and ground covered in puddles. Only females were considered in this study because the sample size was too low for males to conduct statistical analyses. It

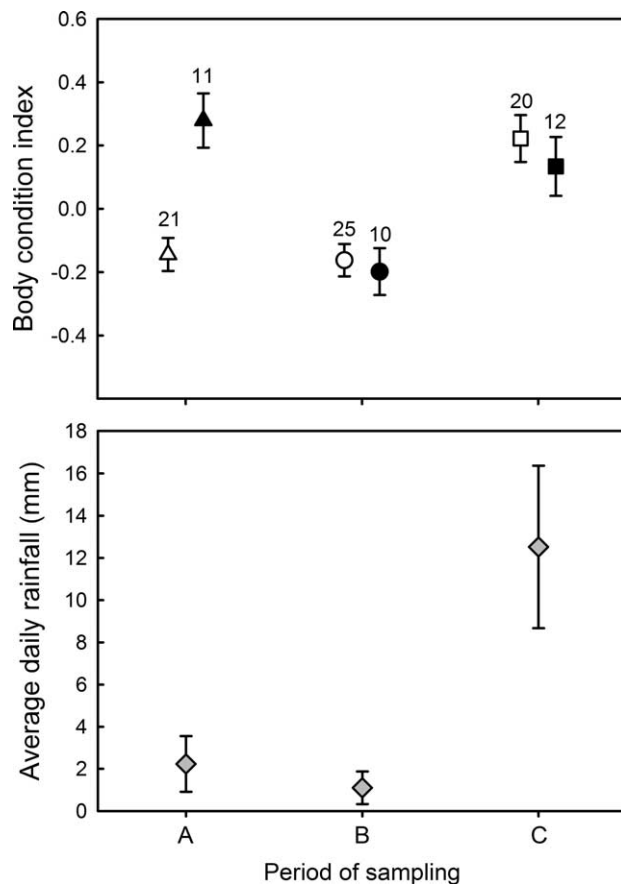


Figure 1. Influence of period of sampling on body condition of female redstarts (mean \pm SE) and average daily rainfall (mm) in 2008 (January–April) at a non-breeding site in Jamaica, West Indies. Birds were sampled in two different habitats (white: scrubs; black: mangroves). Sample sizes are shown above the error bars.

is mainly due to the fact that old males are especially difficult to find in the scrub habitat (Marra 2000). To examine the influence of short-term variations in rainfall on body condition of female redstarts, our initial aim was to sample individuals during the three distinct periods with each period being separated by a 10-d gap. Although we followed this design for the two first periods (A and B), we decided to eliminate the gap between periods B and C because of significant rainfall that occurred at the end of March. This abrupt climatic change represented a biologically relevant way to separate periods B and C and, more importantly, a unique opportunity to examine the influence of abrupt changes in rainfall on changes in body mass of redstarts. In this study, it was not possible to further examine the influence of weekly changes in rainfall abundance on body condition of mangrove and scrub females because of a lack of statistical power. Rainfall data were measured in Black River and provided by the Jamaica Meteorological Service.

Female redstarts were captured with mist-nets, ringed with an aluminum USFWS leg band, aged (HY or AHY) according to Pyle (1997), weighed to the nearest 0.1 g, and measured (wing chord and tail length to the nearest 0.5 mm and tarsus length to the nearest 0.1 mm; Marra and Holmes 2001). For each individual, we calculated body size using factor analysis. Factors were extracted from a principal component analysis performed on the three morphological variables (wing chord, tail length, tarsus length). The first factor accounted for 56% of the variance and all morphological variables were correlated with this factor (correlations, $p < 0.001$ for all variables), which was therefore assumed to represent overall body size. Then, we calculated an index of body condition by using the residuals from a linear regression of body mass against the body size factor ($F_{1,97} = 15.92$, $p < 0.001$, $r = 0.375$). Birds were sampled before the pre-migration process of fattening and no female in our data set had fat deposits, allowing us to reliably estimate body condition (Green 2001). All birds were sampled during a limited daily time frame (between 7:30 am and noon) and we included the time of sampling as an explanatory variable in the models to check for a potential effect of this variable on body condition.

Statistical analyses

All analyses were performed with SAS statistical software (ver. 9.1, SAS Inst.). First, we used a non-parametric Kruskal–Wallis test to test whether rainfall abundance varied between the three periods of sampling (A, B, C). Second, we used generalized linear models with a normal error distribution and an identity link function to test the effect of period of sampling (periods A, B and C), age (HY vs AHY), habitat (mangrove vs scrub) and their interactions on body condition. In addition, we added time of sampling (hour of the day) as an explanatory variable to check whether it affected body condition. We compared all the possible models ($n = 38$ models) since they all correspond to specific plausible biological hypotheses (Burnham and Anderson 2002) and we used a second-order Akaike's information criterion (AICc), which corrects for sample size, to select the best-fitting model while taking into

account parsimony (Burnham and Anderson 2002). We calculated this second-order AICc using the following formula:

$$AICc = -2\log(\text{likelihood}) + 2K + 2K \frac{(K + 1)}{(N - K - 1)}$$

where N is the sample size and K the number of parameters.

The model with the lowest AICc is considered to be the best compromise between model deviance and model complexity (i.e. the number of model parameters). In addition, values for differences in AICc values ($\Delta AICc$) were computed by subtracting the minimum AICc from all candidate model AICc. Differences between AICc values of different models can be used to determine which model provides the most adequate description of the data on the basis of the fewest model parameters: the lower the $\Delta AICc$, the better the fit of the model. Although the model with the lowest AICc is considered the model with the strongest weight of evidence given the data, it is also essential to keep in mind that two models with similar AICc values are equally supported by the data. In addition, we reported an AICc weight (w_i), which reflects the relative likelihood of a specific model being the best-fitting model among all the possible models (Burnham and Anderson 2002). In other words, w_i indicates the probability that the model is the best among the whole set of candidate models. In this study, we decided to arbitrarily report the 5 best-fitting models and the 'null' model in order to show to what extent the best model fits the data better than other models. After model selection was performed, parameter estimates were then used to examine how independent variables such as habitat, period and age affect body condition (Johnson and Omland 2004). Following model selection, posteriori hypotheses were tested by using Wald chi-square statistics. It allowed us testing whether parameter estimates varied between age classes, periods of sampling and habitats. Residual analyses were conducted to check for assumptions of normality (Shapiro–Wilk test) and possible outliers (Cook's distance). There was no indication that normality assumption was violated ($W = 0.987$, $p = 0.486$) and no data point were found to be potential outliers (all Cook's distances were < 0.15 , Cook 1977).

Results

Rainfall differed between the periods of sampling with the most abundant precipitations occurring during the period C (Kruskal–Wallis test, $H = 13.08$, $DF = 2$, $p = 0.001$; Fig. 1).

Model selection results indicated that body condition of female redstarts in our sample was explained by the period of sampling, habitat, and their interaction. These explanatory factors and the interaction were included in all five best-fitting models (Table 1). In addition, the model with the lowest AICc does not include the age factor (Table 1). Although the second best model includes the age factor and has a relatively high AICc weight (Table 1), parameter estimates of this model indicate that body condition does not significantly differ between HY and AHY birds (parameter estimates, mean \pm SE, HY: 0.17 ± 0.09 , AHY: 0.12 ± 0.08 ; $\chi^2 = 0.78$, $p = 0.376$; Fig. 1), confirming that age is not the main determinant of body condition in our study. Time of sampling was not included in the best-fitting model and the best model including this variable had a much larger AICc than the best-fitting model, demonstrating that this variable did not explain body condition (Table 1).

Parameter estimates of the best-fitting model indicate that body condition is better during period A than during period B for mangrove females ($\chi^2 = 15.35$, $p < 0.001$; Fig. 1), but not scrub females ($\chi^2 = 0.05$, $p = 0.830$; Fig. 1). Body condition of both mangrove and scrub females is better during the period C than during period B (mangrove: $\chi^2 = 7.73$, $p = 0.005$; scrub: $\chi^2 = 21.11$, $p < 0.001$; Fig. 1). Body condition of mangrove females is better than that of scrub females during period A ($\chi^2 = 16.66$, $p < 0.001$; Fig. 1), but not during the periods B and C (period B: $\chi^2 = 0.12$, $p = 0.729$; period C: $\chi^2 = 0.75$, $p = 0.385$; Fig. 1).

Discussion

As predicted, we found that the lowest rainfall amounts over the study period were associated with the poorest body condition in female redstarts, supporting the idea that rainfall and water availability are essential to insectivorous passerines during the non-breeding period (Marra and Holberton 1998, Marra et al. 1998, Strong and Sherry 2000, Marra and Holmes 2001, Studds and Marra 2005, 2007, Smith et al. 2010). Importantly, this study is the first

Table 1. Model selection using Akaike's information criterion (AICc) to determine the best model explaining variation in body condition of female redstarts during the non-breeding season. K and w_i refer respectively to the number of parameters and the AICc weight of each model. The five most competitive models (among thirty-eight models) and the model without any explanatory variables ('Null') are represented and ranked according to their AICc.

Dependent variable	Models	K	Log likelihood	AICc	$\Delta AICc$	w_i
Body condition (n = 99)	Period, Habitat, Period \times Habitat	6	-10.94	34.79	0.00	0.453
	Age, Period, Habitat, Period \times Habitat	7	-10.56	36.35	1.56	0.208
	Period, Habitat, Period \times Habitat, Hour	7	-10.97	37.17	2.38	0.138
	Age, Period, Habitat, Age \times Habitat, Period \times Habitat	8	-10.55	38.70	3.91	0.064
	Age, Period, Habitat, Period \times Habitat, Hour	8	-10.5973	38.77	3.98	0.062
	Null	1	-30.61	63.26	28.47	0.000

to demonstrate that body condition (mostly in the form of lean protein reserves) of female redstarts is very plastic during the non-breeding season and can change within a few weeks concomitantly with changes in rainfall and water availability.

In addition, we found that female redstarts with territories in a mangrove habitat were usually in better condition during periods of low rainfall (period A) compared to females living in a scrub habitat during the same period (but see our further discussion on period B). However, body condition did not differ between habitats during an episode of frequent, heavy precipitation (period C). Our results demonstrate that habitat quality and short-term fluctuations in rainfall interact to affect migratory birds during the non-breeding period as previously reported at a longer time-scale frame (intra-seasonal: Marra and Holberton 1998, Marra et al. 1998, Marra and Holmes 2001, Studds and Marra 2005, 2007, inter-annual: Studds and Marra 2007). Specifically, it demonstrates that a habitat of high quality can reduce the deleterious effect of a temporary reduction in rainfall abundance on body condition (period A), but, also, that a habitat of low quality does not constrain individuals when environmental conditions are optimal (heavy rainfall, period C). Although food abundance was not measured in our study of redstarts, these habitat-dependent variations in body condition are very likely to result from changes in food abundance because of its pivotal role in controlling body condition of migratory birds during the non-breeding period (Studds and Marra 2005, Brown and Sherry 2006, Newton 2006, Smith et al. 2010). In insectivorous passerines, food abundance directly depends on the presence of water and humidity, which is essential to maintain insect productivity (Dugger et al. 2004, White 2008, Smith et al. 2010). In addition, drought may also have affected more directly body condition of female redstarts. These birds may have suffered from the lack of water and may have needed to increase their displacement and their energy expenditure to have access to water. Therefore, the ability of mangrove habitat to lessen the impact of a reduction in rainfall on body condition probably results from its structure, which permits the retention of water despite the absence of rainfall (Studds and Marra 2005, 2007).

After several weeks of low rainfall (period B), body condition of mangrove females declined to a level similar to that of scrub females. Therefore, we only found an ameliorating effect of habitat quality on body condition in female redstarts during the period A, and a prolonged drought results in a similar body condition for birds from both habitats (period B). Importantly, our study therefore shows for the first time that the timing of environmental perturbation is important, but so is the duration of that perturbation. This result could however appear surprising because previous studies have reported that habitat of high quality can mitigate the deleterious effect of low rainfall on the body condition of redstarts even if this perturbation lasted several months (Marra and Holberton 1998, Studds and Marra 2005). Thus, Marra and Holmes (2001) reported that mangrove redstarts were in better condition than scrub redstarts at the end of very dry season. The pattern we reported in this study may result from the specific conditions in 2008, when the mangroves remained

largely submerged during the whole study period although edge areas became dry during the period B and, thus, may have suffered a slightly reduction in insect abundance. Interestingly, all the mangrove females were found in these edge areas in our study, probably because they are usually excluded from the deeper, central parts of the mangroves by dominant males (Marra 2000). Although this may potentially explain why body condition of mangrove female redstarts decreased during period B, it then remains unclear why this pattern was not apparent in drier years (Marra and Holberton 1998, Marra and Holmes 2001, Studds and Marra 2005). This may result from other environmental factors that may have varied between years such as density-dependent processes. Because of unusual wet conditions in 2008, we can also speculate that the insect community might have differed from other years and might have been more sensitive to this short-term dry episode (period B). This would explain why mangrove females showed such a reduction in body condition during this period. Although food availability data (food abundance and insect diversity) would have been necessary to confirm this hypothesis, our results support the idea that the capacity of a habitat to act as a buffer against a climatic perturbation is limited in time because the perturbation eventually affects the characteristics of the habitat itself and, thus, reduces its suitability (Löhms 2003). Our study, consistent with other studies from this system, suggests therefore that habitat suitability is a dynamic parameter which depends on habitat composition and structure (mangrove vs scrub) but that it can also be affected by environmental perturbations (rainfall abundance). This supports the idea that habitat and other environmental variables, such as density or predation risk, can interact to affect wild vertebrates (Strong and Sherry 2000, Löhms 2003, Zanette et al. 2006, Byholm and Kekkonen 2008).

In our study, age did not affect body condition in non-breeding female redstarts during any of the three periods, suggesting that non-breeding birds do not perform better in case of short-term perturbations (a few weeks) when they become older or more experienced (the 'constraint hypothesis', Curio 1983). However, one must note that the effect of age on individual performances could be masked by selective processes (Mauck et al. 2004). Indeed, migration is definitely a demanding life-history stage (Sillert and Holmes 2002), and the first migration probably acts as a filtering period leading to the selection of high-quality young individuals that perform well on the non-breeding grounds despite their young age and their lack of experience. Moreover, age may be beneficial to redstarts through dominance processes. Young redstarts can become excluded from higher-quality, mangrove habitats by experienced redstarts and are forced to establish territories in lower-quality scrub (Marra 2000). However, we did not find any effect of age on body condition in either mangrove or scrub habitats, suggesting that older female redstarts are not better able to cope with a reduction of rainfall abundance than young individuals when established in a specific habitat. Thus, consistent with previous studies (Marra and Holmes 2001, Perez-Tris and Telleria 2002, Brown and Sherry 2006), age or the experience on the non-breeding grounds does not provide an intra-habitat advantage to non-breeding passerines in terms of resource acquisition, at least in this extremely wet year.

Conclusion

Here, we show that the combined effects of habitat and monthly fluctuations in rainfall interact to affect body condition of non-breeding female redstarts. This result confirms that habitat suitability depends on both non-breeding habitat type (mangrove vs scrub) and their respective responses to rainfall conditions (Marra and Holberton 1998, Marra et al. 1998, Marra and Holmes 2001, Studds and Marra 2005, 2007, Smith et al. 2010). Importantly, we also demonstrate for the first time that body mass of female redstarts can change rapidly in response to the short-term environmental variations that can occur over the non-breeding season. To better understand the proximate mechanisms that drive individual differences in body condition of migratory birds, future studies should examine the combined influence of rainfall and habitat structure (vegetation, location) on body condition but also on direct suitability measurements of specific non-breeding territories (i.e. food abundance, temperature, humidity).

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References

- Altwegg, R., Roulin, A., Kestenholz, M. and Jenni, L. 2006. Demographic effects of extreme winter weather in the barn owl. – *Oecologia* 149: 44–51.
- Angelier, F., Weimerskirch, H., Dano, S. and Chastel, O. 2007a. Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. – *Behav. Ecol. Sociobiol.* 61: 611–621.
- Angelier, F., Moe, B., Weimerskirch, H. and Chastel, O. 2007b. Age-specific reproductive success in a long-lived bird: do older parents resist stress better? – *J. Anim. Ecol.* 76: 1181–1191.
- Barbraud, C. and Weimerskirch, H. 2005. Environmental conditions and breeding experience affect costs of reproduction in blue petrels. – *Ecology* 86: 682–692.
- Bauer, S., Gienapp, P. and Madsen, J. 2008. The relevance of environmental conditions for departure decision changes en route in migration geese. – *Ecology* 89: 1953–1960.
- Beauplet, G. and Guinet, C. 2007. Phenotypic determinants of individual fitness in female fur seals: larger is better. – *Proc. R. Soc. B* 274: 1877–1883.
- Brown, D. R. and Sherry, T. W. 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. – *Oecologia* 149: 22–32.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference. – Springer.
- Byholm, P. and Kekkonen, M. 2008. Food regulates reproduction differently in different habitats: experimental evidence in the goshawk. – *Ecology* 89: 1696–1702.
- Cook, R. D. 1977. Detections of influential observation in linear regression. – *Technometrics* 19: 15–18.
- Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J. and Grenfell, B. T. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. – *Science* 292: 1528–1531.
- Curio, E. 1983. Why do young birds reproduce less well? – *Ibis* 125: 400–404.
- Dugger, K. M., Faaborg, J., Arendt, W. J. and Hobson, K. A. 2004. Understanding survival and abundance of overwintering warblers: does rainfall matter? – *Condor* 106: 744–760.
- Garel, M., Loison, A., Gaillard, J. M., Cugnasse, J. M. and Maillard, D. 2004. The effects of a severe drought on mouflon lamb survival. – *Proc. R. Soc. B* 271: 471–473.
- Gordo, O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. – *Clim. Res.* 35: 37–58.
- Green, A. J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? – *Ecology* 82: 1473–1483.
- Holberton, R. L. and Able, K. P. 2000. Differential migration and an endocrine response to stress in wintering dark-eyed juncos (*Junco hyemalis*). – *Proc. R. Soc. B* 267: 1889–1896.
- Johnson, J. B. and Omland, K. S. 2004. Model selection in ecology and evolution. – *Trends Ecol. Evol.* 19: 101–108.
- Löhms, A. 2003. Are certain habitats better every year? A review and a case study on birds of prey. – *Ecography* 26: 545–552.
- Marra, P. P. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the non-breeding season. – *Behav. Ecol.* 3: 299–308.
- Marra, P. P. and Holberton, R. L. 1998. Corticosterone levels as indicators of habitat quality: effect of habitat segregation in a migratory bird during the non-breeding season. – *Oecologia* 116: 284–292.
- Marra, P. P. and Holmes, R. T. 2001. Consequences of dominance-mediated habitat segregation in a migrant passerine bird during the non-breeding season. – *Auk* 118: 92–104.
- Marra, P. P., Hobson, K. A. and Holmes, R. T. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. – *Science* 282: 1884–1886.
- Mauck, R. A., Huntington, C. E. and Grubb Jr, T. C. 2004. Age-specific reproductive success: evidence for the selection hypothesis. – *Evolution* 58: 880–885.
- McNamara, J. M. and Houston, A. I. 1996. State-dependent life-histories. – *Nature* 380: 215–221.
- Moe, B., Langseth, I., Fyhn, M., Gabrielsen, G. W. and Bech, C. 2002. Changes in body condition in breeding kittiwakes *Rissa tridactyla*. – *J. Avian Biol.* 33: 225–234.
- Mrosovsky, N. and Sherry, D. F. 1980. Animal anorexias. – *Science* 207: 837–842.
- Newton, I. 2006. Can condition experienced during migration limit the population levels of birds? – *J. Ornithol.* 147: 146–166.
- Perez-Tris, J. and Telleria, J. L. 2002. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implication for the evolution of avian migration. – *J. Anim. Ecol.* 71: 211–224.
- Pyle, P. 1997. Identification guide to North American birds. – Slate Creek Press, Bolinas, USA.
- Reudink, M. W., Studds, C. E., Marra, P. P., Kyser, T. K. and Ratcliffe, L. M. 2008. Plumage brightness predicts non-breeding season territory quality in a long-distance migratory songbird, the American redstart *Setophaga ruticilla*. – *J. Avian Biol.* 40: 34–41.
- Reudink, M. W., Marra, P. P., Kyser, T. K., Boag, P. T., Langin, K. M. and Ratcliffe, L. M. 2009. Non-breeding season events influence sexual selection in a long-distance migratory bird. – *Proc. R. Soc. B* 276: 1619–1626.

- Schaub, M. and Jenni, L. 2001. Variation of fuelling rates among sites, days and individuals in migrating passerine species. – *Funct. Ecol.* 15: 584–594.
- Sillett, T. S. and Holmes, R. T. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. – *J. Anim. Ecol.* 71: 296–308.
- Smith, J. A. M., Reitsma, L. R. and Marra, P. P. 2010. Moisture as a determinant of habitat quality for a nonbreeding neotropical migratory songbird. – *Ecology* 91: 2874–2882.
- Sperry, J. H. and Weatherhead, P. J. 2008. Prey-mediated effects of drought on condition and survival of a terrestrial snake. – *Ecology* 89: 2770–2776.
- Strong, A. M. and Sherry, T. W. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. – *J. Anim. Ecol.* 69: 883–895.
- Studds, C. E. and Marra, P. P. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. – *Ecology* 86: 2380–2385.
- Studds, C. E. and Marra, P. P. 2007. Linking fluctuations in rainfall to non-breeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. – *Clim. Res.* 35: 115–122.
- Trites, A. W. and Donnelly, C. P. 2003. The decline of Steller sea lions *Eumotopias jubatus* in Alaska: a review of the nutritional stress hypothesis. – *Mammal. Rev.* 33: 3–28.
- Weladji, R. B., Loison, A., Gaillard, J. M., Holand, O., Mysterud, A., Yoccoz, N. G., Nieminem, M. and Stenseth, N. C. 2008. Heterogeneity in individual quality overrides costs of reproduction in female reindeer. – *Oecologia* 156: 237–247.
- White, T. C. R. 2008. The role of food, weather and climate in limiting the abundance of animals. – *Biol. Rev.* 83: 227–248.
- Zanette, L., Clinchy, M. and Smith, J. N. M. 2006. Combined food and predator effects on songbird nest survival and annual reproductive success: results from a bi-factorial experiment. – *Oecologia* 147: 632–640.