Ecological factors affecting foraging behaviour during nestling rearing in a high-elevation species, the White-winged Snowfinch (*Montifringilla nivalis*)

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During breeding, parents of avian species must increase their foraging efforts to collect food for their offspring, besides themselves. Foraging trips are thus a key aspect of the foraging ecology of central-place foragers when rearing their offspring. However, studies of the foraging ecology of high-elevation specialists inhabiting harsh environments are scarce. Here we report for the first time quantitative information on ecological determinants of foraging trips in the White-winged Snowfinch (*Montifringilla nivalis*), a high-elevation specialist threatened by climate warming. We focused on seasonal, meteorological, habitat and social factors affecting distance and duration of foraging trips performed during nestling rearing, recorded by visual observations in the Italian Alps. Based on 309 foraging trips from 35 pairs, we found that trips lasted 6.12 min and foraging areas were located at 175 m from the nest site on average. Trip duration was affected by snow cover (longer at intermediate cover), distance travelled and wind, while distance travelled was affected by snow cover (being higher at intermediate cover) and trip duration. Foraging individuals thus travelled farther and spent more time at areas characterized by intermediate snow cover, implying the presence of snow margins. It is likely that at such snow patches/margins snowfinches collected food for self-maintenance, besides that for their offspring, or collected more food items. Any reduction of snow cover during the breeding season, as expected under current climate warming, will severely alter foraging habitat suitability. Conserving suitable foraging habitats in the nest surroundings will be crucial to buffer such negative impacts.

1. Introduction

During the breeding phase, parents of altricial animal species must increase their foraging efforts to collect food for their offspring, in addition to that required for their self-maintenance (Grémillet 1997, Collins *et al.* 2016). Investigating variation in foraging behaviour during the offspring rearing period is thus pivotal for assessing time and energy budgets and the determinants of fitness. Several studies have therefore evaluated ecological factors (e.g., habitat, weather, and social effects) affecting foraging behaviour of central-place foraging species. The key feature of foraging behaviour in central-place foragers during the offspring rearing period is represented by foraging trips, during which individuals leave from the place when offspring are hidden/located (typically the den or nest site), explore the surrounding of the breeding site to search for food, collect it, and then bring it back to the offspring.

Studies investigating foraging trips characteristics and factors affecting them have been performed on a wide array of animal species, ranging from marine to terrestrial vertebrates and invertebrates. Resource abundance and availability, environmental conditions, and density-dependent factors have been found to affect foraging trips length and duration (Cresswell *et al.* 2000, Westphal *et al.* 2006, Elliott 2009, Boyd *et al.* 2014, Collins *et al.* 2016, Dunn *et al.* 2017, Hemberger & Gratton 2018). However, studies on high-elevation species are much scarcer and we are not aware of studies considering bird species exclusively dwelling in high-elevation, alpine environments.

High-elevation specialists are particularly interesting as they live under harsh conditions, with generally scarce resources, and require adaptations to extreme environments (Martin & Wiebe 2004, Lu *et al.* 2009, Gobbi *et al.* 2017). The extreme environmental conditions these species are experiencing may strongly affect foraging behav-
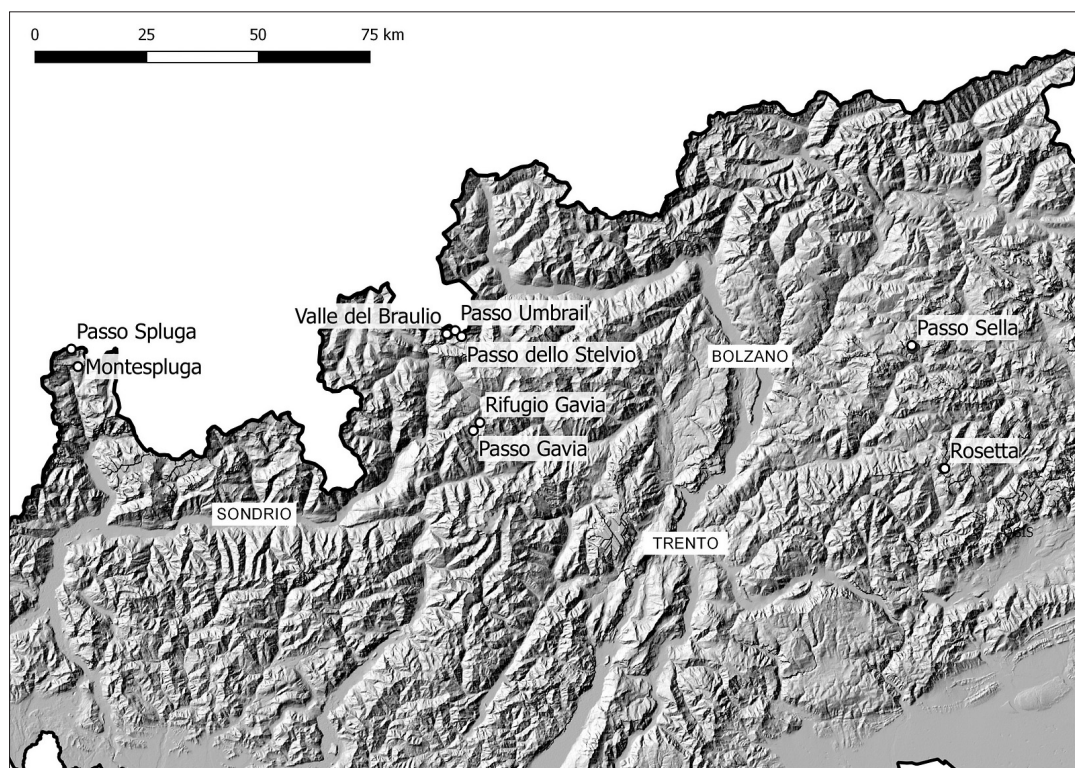

Fig. 1. Map of the study sites within the Italian Alps. The location of some major towns is also shown to help interpretation.

iour, as they may severely affect prey availability and/or the costs of transportation. This is especially the case during reproduction, when parents may be forced to carefully allocate resources to self-maintenance vs. parental care, and foraging decisions may therefore have potentially important consequences for fitness (Martin & Wiebe 2004, Camfield and Martin 2009, Liang *et al.* 2018).

Apart from habitat and environmental factors, foraging behaviour may be influenced by social behaviour. For instance, many species breed colonially, sharing resources and space, with broad ecological and evolutionary implications (Danchin *et al.* 2008). On the one hand, colonial breeding may entail advantages because of improved exploitation of patchy and ephemeral food resources by means of e.g., local enhancement processes, whereby individuals from a given colony site are attracted by foraging aggregations o conspecifics, or shared costs of predator defence (e.g., Evans *et al.*, 2016). On the other hand, colonial breeding may increase the degree of intraspecific competition for food among colony members, because of progressive depletion of food resources in the colony surroundings (the so-called "Ashmole's halo" effect; Ashmole 1963), which may affect foraging decisions (Cecere *et al.* 2018).

Here, we investigate the seasonal, meteorological, habitat and social factors affecting foraging behaviour in breeding White-winged Snowfinches (*Montifringilla nivalis*). The White-winged Snowfinch is a high-elevation specialist species with a scattered breeding distribution in the main Eurasian temperate and temperate-warm mountains, below the 10°C isotherm (Cramp & Perrins 1994). It generally breeds above the treeline (mostly above 2,000 m a.s.l. in Europe) in cavities within rocky areas, buildings, pylons, etc. Breeding pairs may reproduce solitarily or in neighbourhood groups, usually comprising up to 10 pairs (Cramp & Perrins 1994).

Like many other high-elevation specialist species (Scridel *et al.* 2018), the Snowfinch is severely threatened by climate warming at several spatial scales; distribution models at large scales predict severe range shrinkage in the next decades (Brambilla *et al.* 2016, 2017b), and foraging habitat selection at a finer scale reflects a strong link with snow (especially snow margins), short

Table 1. Number of Withe-winged Snowfinch nests monitored within each study area (see Fig. 1 for the geographical location of the study areas) in the study years.

Site	Elevation of nest sites (m a.s.l.)	Number of monitored nests
Passo Spluga	2,114	1
Montespluga	1,880	1
Valle del Braulio	2,310	5
Passo Umbrail	2,488	1
Passo dello Stelvio	2,692	5
Passo Gavia	2,613	2
Rifugio Gavia	2,545	2
Rosetta	2,544	1

ground vegetation and colder microsites (Brambilla *et al.* 2017a, Resano-Mayor *et al.* 2019); structural suitability of foraging microhabitat is also predicted to decline in the future because of climate change (Brambilla *et al.* 2018a). We focus on identifying the ecological factors potentially affecting the two main characteristics of foraging trips (distance and duration) during the energy-demanding offspring rearing period, with special reference to those variables that are potentially affected by changing high-elevation climatic conditions, such as ambient temperature, rainfall and snow cover, and to habitat management, such as the occurrence of grazing activity, which may improve foraging habitat suitability for the study species and other high-altitude passerines (Brambilla *et al.* 2018a).

2. Methods

2.1. Study area and data collection

We recorded foraging trips (individuals followed from nest-leaving to return to the nest) of breeding Snowfinch pairs during the nestling rearing period in the Italian Alps (Fig. 1) in June–July 2015 (18 nests) and 2016 (17 nests), largely within the same areas (Table 1). Observations were conducted by two observers, equipped with 10x binoculars and positioned in proximity of active nests that, thanks to their location, allowed an easy observation of the parents involved in nestling rearing without

causing alterations of the birds' behaviour. Observations were carried out when nestlings were ca. 5–18 days old. Each nest was surveyed during one day, recording an average of 8.77 ± 5.28 (SD) foraging trips (range 2–30) per nest.

In a limited number of cases, it was not possible to consistently follow foraging adults for the entire trip; these observations were discarded. Foraging positions were recorded by means of a GPS device, or by mapping the exact location on a highly detailed aerial photograph (mapping error < 5 m with both methods). Foraging positions were defined as the first position where a prey was collected, or the last position of the individual before it returned to the nest when prey collection was not observed, as snowfinches usually fly back to the nest after collecting a prey (Brambilla *et al.* 2017a, 2018a). For each foraging trip we recorded leaving and returning time (nearest min), cloud cover (categorical: sunny, overcast, partly overcast), wind (categorical: strong, weak or moderate, calm), temperature, rainfall (categorical: absent, weak, abundant). For each foraging position we recorded the distance from the nest site (nearest m) and the detailed habitat cover within a 5-m radius according to the protocols reported in Brambilla *et al.* (2018a).

Briefly, we estimated the percentage cover of snow, water, rock, boulders, scree, sand, bare ground, grassland, shrubs, unpaved roads, paved roads, buildings, and other habitats (Brambilla *et al.* 2018a). We also recorded evidence of ongoing or recent grazing activity (presence of grazers or fresh dungs) and measured the height of the grassland sward at five points per each location (foraging point plus four points at 2.5 m from the foraging position, along the four cardinal directions). Air temperature was recorded at hourly intervals using a mercury thermometer placed under constant shade on a pole at 1.5 m above the soil at the observation site. We assigned to each trip the closest hourly temperature value.

Finally, for each foraging position, we calculated solar radiation (predicted radiation at 21st June; Brambilla *et al.* 2018a) and slope according to a 5-m resolution DEM (Digital Elevation Model), using commands r.sun and slope.aspect in GRASS (Neteler *et al.* 2012). Nests sites were characterized as isolated (no active nest within 400 m) or clustered (at least one other active nest oc-

curring within 400 m). Birds breeding in clusters might achieve information on suitability of foraging sites by observing the behaviour of their neighbours, whereas birds breeding in isolated sites can not benefit from intraspecific copying. The 400 m-distance threshold was set in order to identify those pairs which could show a high overlap of shared foraging ground, considering the radius of the area usually exploited around the nest (i.e., 300 m, Brambilla *et al.* 2017a).

2.2. Statistical analyses

We related foraging trip duration (after removing outliers; see Results) to the weather and environmental predictors, coloniality (single nest vs. cluster of breeding pairs) and distance of foraging location from nest (distance travelled) by means of Linear Mixed Models (LMMs), with pair identity and year set as a random intercept effects. All continuous variables were standardized (mean = 0 and SD = 1) before analyses. To reduce model complexity and limiting multicollinearity, we divided predictors into four groups: habitat, seasonal and weather, topography, sociality, which were modelled separately.

The habitat predictors included various categories of land-cover (apart from anthropized areas, removed from models as equal to 0 in most foraging plots), and sward height variables; snow cover was included with both the linear and the squared term because of the previously reported preference for snow margins (i.e. areas with intermediate snow cover) shown by snowfinches (Strinella *et al.* 2007, Brambilla *et al.* 2018a); as the inclusion of the squared term too was supported by the habitat model, we then retained it also in the final synthetic model (see below). Season and weather predictors comprised time of the day, temperature, cloud cover and wind. Topographic variables included distance travelled, elevation, solar radiation and slope; sociality was used to distinguish between isolated or clustered sites (binomial factor).

For each group of predictors, we built models with breeding pair and year as random factors. Then, we performed the following model selection: we ranked all possible models within each group by means of the AICc (Akaike's informa-

Table 2. Best supported models (ΔAICc < 2) and associated parameter estimates for trip duration in nest-ling-rearing White-winged Snowfinches, considering the different variable groups and the synthetic model. For categorical factors, the + indicates the inclusion in the model. Time means time of the day.

Habitat

Intercept	Shrub	Snow	Snow^2	Water	df	logLik	AICc	Delta	Weight
6.61		1.49	–0.49		6	–831.75	1675.8	0	0.26
6.63	0.27	1.51	–0.48		7	–831.12	1676.6	0.83	0.17
6.55		1.37	–0.44	0.18	7	–831.48	1677.3	1.56	0.12

Season and weather

Intercept	Date	Clouds	Wind	Time	df	logLik	AICc	Delta	Weight
6.09	0.62			0.43	6	–834.62	1681.5	0	0.26
6.53	0.49		+	0.48	8	–832.85	1682.2	0.67	0.19
6.08	0.60				5	–836.07	1682.3	0.81	0.18
6.71	0.58	+		0.49	8	–833.07	1682.6	1.11	0.15
6.47			+	0.45	7	–834.24	1682.8	1.33	0.14

Topography and distance travelled

Intercept	Distance				df	logLik	AICc	Delta	Weight
6.12	1.21				5	–826.27	1662.7	0	1

Sociality

Intercept	Sociality				df	logLik	AICc	Delta	Weight
6.11					4	–838.66	1685.4	0	0.63
6.36	+				5	–838.16	1686.5	1.07	0.37

Synthetic

Intercept	Date	Distance	Wind	Time	Snow	Snow^2	df	logLik	AICc	Delta	Weight
6.69		1.14	+		1.29	–0.37	9	–816.28	1651.2	0.47	0.22
6.77	0.23	1.06	+		1.41	–0.43	10	–815.91	1652.6	1.87	0.11
6.69		1.14	+	0.18	1.19	–0.32	10	–815.95	1652.6	1.95	0.11

tion criterion corrected for small sample size) and considered as best supported those models which had ΔAICc < 2 from the best fitting model. Then, we selected from each group all variables included in the best supported models after the exclusion of uninformative parameters, i.e. those variables which, when included, resulted in an increase of the AICc value (Arnold 2010, Jedlikowski *et al.* 2016), and built a final synthetic model according to the same AICc-based procedure (see e.g. Assandri *et al.*, 2018).

The same procedure (also based on LMMs) was applied to modelling factors affecting distance travelled during foraging trips (with the inclusion of trip duration instead of distance travelled in the same variable group). For both duration and dis-tance models, the final step identified a single best supported model (all others models after the exclu-sion of the uninformative parameters had ΔAICc>2).

3. Results

We recorded 309 foraging trips from 35 breeding pairs (134 from 18 pairs in 2015, 175 from 17 pairs in 2016). Foraging trips lasted on average 6.12 min (range 1–42); all but two foraging trips lasted ≤ 21 min; two trips of 37 and 42 min were considered outliers and removed from the analyses. The dis-tance travelled was on average 175 m (range 0–1008), and 86% of the foraging locations were within 300 m of the nest site.

Concerning foraging trip duration, snow cover (linear and quadratic term) was the only habitat variable included in supported models (ΔAICc<2; Table 2). In the season and weather group, relevant predictors were date, wind and time of the day. In the topography group, distance travelled was the only supported factor; finally, the model including sociality was less supported than the null model (Table 2). We therefore built a synthetic model
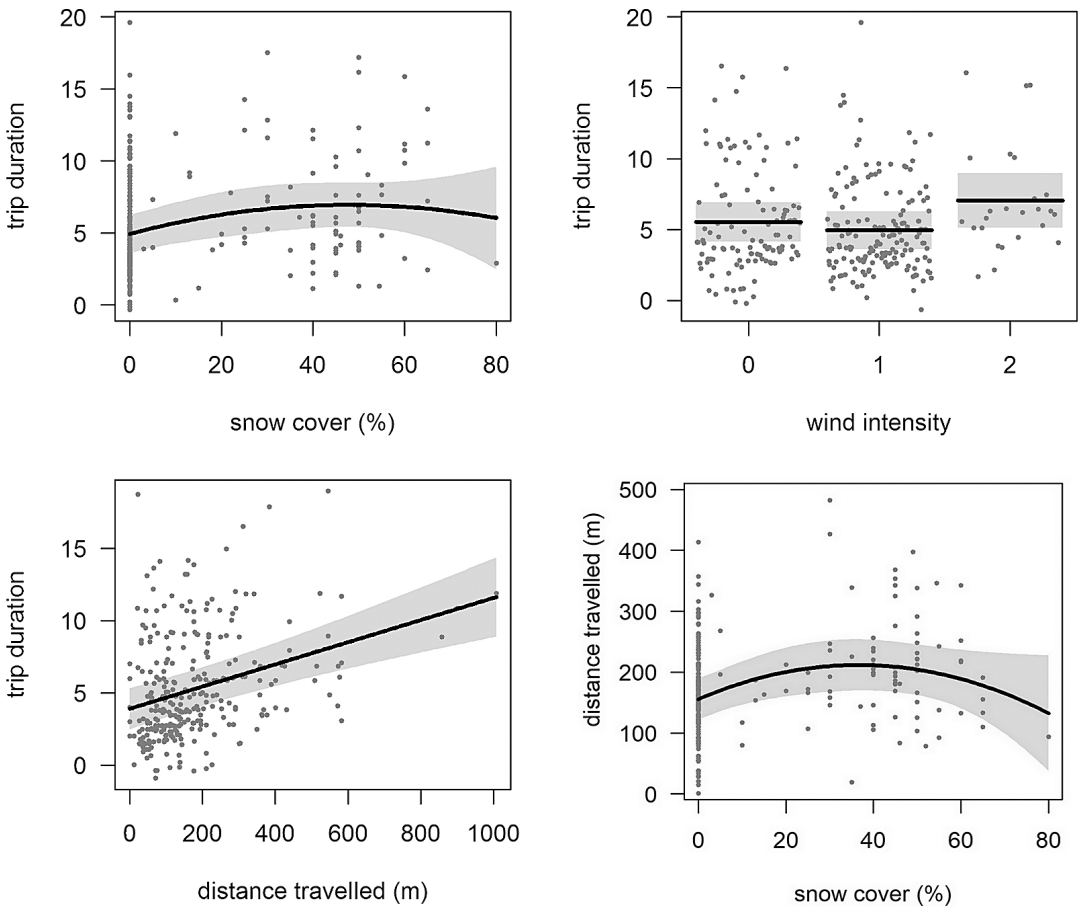
Fig. 2. Duration of foraging trips (in min) in White-winged Snowfinches in relation to snow cover (percentage cover over the 5-m radius surrounding the foraging position), wind intensity (0: calm; 1: weak or moderate; 2: strong), and distance travelled (m) in relation to snow cover (lower right).

testing the above listed six supported variables; the final model ($R^2 = 0.17$) included distance travelled, wind and snow cover (Table 2, Fig. 2).

Concerning the distance travelled during a foraging trip, the only habitat factor included in supported models (ΔAICc<2) was snow cover (linear and quadratic term; Table 3). In the season and weather group, the only relevant predictor was time of the day. In the topography and duration group, the only relevant factor was trip duration; finally, the model including sociality was less supported than the null model. We therefore built a synthetic model testing snow cover (and its quadratic term), time of the day and trip duration; the final model ($R^2 = 0.46$) for distance travelled included only trip duration (21.36 ± 5.41) and snow cover (linear term: 42.47 ± 13.24; quadratic term:

-17.45 ± 7.64; intercept = 190.95 ± 18.40); distance travelled was higher at intermediate snow cover (Fig. 2) and with higher duration.

4. Discussion

Our study provides the first quantitative information on the duration and distance travelled of foraging trips, and on factors affecting them, in a high-elevation avian specialist. Snowfinches mostly foraged within 300 m of the nest site, as previously reported by studies carried out in the Alps (Brambilla *et al.* 2017a, 2018a) and the Apennines (Strinella *et al.* 2007). Foraging trips mostly lasted less than 20 minutes, with few rare exceptions. The duration of foraging trips was af-

Table 3. Best supported models (ΔAICc < 2) and parameter estimates for distance travelled in nestling-rearing White-winged Snowfinches, considering the different variable groups and the synthetic model. For categorical factors, the + indicates the inclusion in the model. Time means time of the day

Habitat

Intercept	Shrub	Snow	Snow^2	Water	df	logLik	AICc	Delta	Weight
194.8		51.36	−20.05		6	−1811.29	3634.9	0	0.4
196.4		55.17	−21.32	−8.09	7	−1810.54	3635.5	0.6	0.29

Season and weather

Intercept	Date	Cloud	Wind	Time	df	logLik	AICc	Delta	Weight
176.2				17.33	5	−1816.91	3644	0	0.24
163.2		+	+	18.02	9	−1812.84	3644.3	0.26	0.21
165.6	21.21	+	+	17.91	10	−1811.8	3644.3	0.32	0.2
175.4	8.42			15.83	6	−1816.5	3645.3	1.26	0.13
159.8		+		15.06	7	−1815.55	3645.5	1.45	0.12
191.5	26.05		+	22.28	8	−1814.56	3645.6	1.58	0.11

Topography and duration

Intercept	Duration				df	logLik	AICc	Delta	Weight
173.3	25.05				5	−1809.14	3628.5	0	1

Sociality

Intercept	Sociality				df	logLik	AICc	Delta	Weight
174.8					4	−1819.48	3647.1	0	0.74
173.4	+				5	−1819.47	3649.2	2.06	0.26

Synthetic

Intercept	Duration	Time	Snow	Snow^2	df	logLik	AICc	Delta	Weight
191	21.36		42.47	−17.45	7	−1803.69	3621.8	0	0.44
190.6	20.97	9.11	39.19	−16.35	8	−1802.96	3622.4	0.64	0.32

fected by different ecological factors, including snow cover and wind conditions. The distance travelled was affected by snow cover, being highest at intermediate snow cover. Duration affected distance travelled and *vice versa*; the pattern we found suggested both a direct effect of snow-cover on both, and an additional indirect effect, with the search for intermediate snow-cover resulting in higher distance travelled, in turn resulting in a longer trip duration.

As expected, longer-distance trips required more time than shorter ones. Breeding individuals may cover greater distances because of a lack of suitable prey or foraging habitats close to the nest (Cresswell *et al.* 2000, Westphal *et al.* 2006). When they in fact occurred in nest proximity, breeding pairs may forage in the immediate surrounding of the nest (including on the ground just below it, as observed in some instances in our study).

Strong wind also increased foraging trip duration. Wind is a key factor for foraging birds, as it

could affect energetic costs of flight (Furness & Bryant 1996) and even lead to changes in distribution and life-history traits in species heavily relying on winds, such as seabirds (Weimerskirch *et al.* 2012). Evidence of wind effect on terrestrial birds during reproduction is scant, but it is well known that strong winds can lower the number of active insects, and this could result in a longer time required to find preys by breeding snowfinches. In addition, strong wind may impair flight ability in this small species. Surprisingly, grassland cover and sward height, which are key components of foraging habitat selection for breeding snowfinches (Brambilla *et al.* 2017a, 2018a), did not affect trip characteristics. This could be due to the fact that suitable grassland are more evenly distributed around the nests, potentially also because nest-site selection could be driven by their availability.

Snow cover stands out as a crucial factor for breeding snowfinches. It is one of the most impor-

tant determinants of microhabitat selection by nestling rearing snowfinches, which are associated with snow patches and especially with snow margins (Brambilla *et al.* 2017a, 2018a). Our work confirms the importance of snow cover, which affected both trip duration and trip length according to a quadratic effect. Interestingly, suitable microhabitat conditions determined by snow cover (Brambilla *et al.* 2017a, 2018a, Resano-Mayor *et al.* 2019) were associated with longer foraging trip duration. We assume that foraging in suitable habitats does not hamper prey collection; this pattern could be due to the fact that suitable sites with intermediate snow cover are located relatively far from nests, this increasing distance travelled and in turn duration. Given that snow cover had an important effect on trip duration even when taking into account the distance travelled, it is also very likely that when snowfinches forage on snow-covered areas, such as snow patches and, especially, their margins, which are particularly profitable for them (Muscio *et al.* 2005, Strinella *et al.* 2007, Brambilla *et al.* 2018a, Resano-Mayor *et al.* 2019), they also collect food for self-maintenance, or collect a higher number of items to be delivered to the nest.

Other bird species have been reported to spend more time on foraging trips in most profitable habitats to collect preys for self-maintenance during the nestling rearing period. In Blue Tits *Cyanistes caeruleus*, parents experiencing food supplementation partly consumed the additional food, and made longer foraging trips (Grieco 2002). Similarly, we can hypothesize that snowfinches exploiting prey-rich microhabitats may take more time to collect food for self-maintenance. The fact that also distance travelled peaked at intermediate snow cover values suggests that snowfinches may increase the length of foraging trips to reach the most suitable conditions, i.e., snow margins.

The expected reduction of snow cover during the Snowfinch breeding season, mostly due to earlier snow melt in spring (Klein *et al.* 2016), will severely impact on foraging habitat suitability for the species (Brambilla *et al.* 2018a); our results add further concerns, as the occurrence of snow margins emerged as a main driver of foraging behaviour, affecting both trip duration and distance travelled; in addition, the reduction of snow cover and hence of snow margins might limit a key habitat

for parents' self-maintenance during nestling rearing.

Our study finally highlights the importance of conserving suitable foraging habitat (Brambilla *et al.* 2018a) in the surroundings of Snowfinch nest sites to reduce energy expenditure during foraging and buffer the potential negative impact of earlier snow melting (Strinella *et al.* 2007, Brambilla *et al.* 2017a, 2018a, 2018b).

Lumivarpusen ravinnonhankintaan vaikuttavat ympäristötekijät

Lintuemojen pitää kasvattaa panostustaan ravinnonhankintaan lisääntymisaikana, jotta ne voivat täyttää poikasten ravinnontarpeen, itsensä lisäksi. Ravinnonhankintamatkat ovat tärkeä osa reviirilintujen ekologiaa. Vuoristoalueille erikoistuneiden lajien ravinnonhankintaekologiasta on kuitenkin vain vähän tutkimustietoa.

Tässä tutkimuksessa kvantifioimme ensimmäistä kertaa lumivarpusten ravinnonhankintaan vaikuttavia ympäristötekijöitä. Selvitimme säiden, habitaatin, sosiaalisen ympäristön ja vuodenaikaisen vaihtelun vaikutusta ravinnonhankintamatkojen pituuteen ja kestoon. Tutkimus perustui havainnointiin Italian Alpeilla. Seurasimme 35:tä paria ja 309:ää matkaa, joiden keskimääräinen kesto oli 6,12 min ja etäisyys 175 m pesästä.

Matkan kestoon vaikuttivat lumipeitteen määrä (kesto kasvoi keskimääräisellä lumenpaksuudella) matkan pituus ja tuuliolosuhteet. Matkan pituuteen vaikuttivat lumen paksuus (pidempi matka keskimääräisellä lumenpaksuudella) ja matkan kesto. Ruokailevat yksilöt matkustivat pidempään ja käyttivät enemmän aikaa alueilla, joilla oli keskimääräinen lumenpaksuus, ja jotka todennäköisesti olivat lumen reuna-alueita. Todennäköisesti lumivarpuset keräsivät ruokaa sekä itselleen että poikasilleen tällaisilla lumilaikuilla, vaihtoehtoisesti ne keräsivät keskimäärin enemmän ravinto-

kohteita. Lumenpaksuuden ja peittävyyden väheneminen ilmastonmuutoksen seurauksena voi täten huomattavasti heikentää elinympäristöjen laatua. Pesien ympärillä olevien habitaattien suojeleminen onkin tärkeää haitallisten vaikutusten ehkäisemiseksi.

References

Arnold, T.W. 2010: Uninformative Parameters and Model Selection Using Akaike Information Criterion. — Journal of Wildlife Management 74: 1175–1178.

Ashmole, N.P. 1963: The regulation of numbers of tropical oceanic birds. — Ibis 103: 458–473.

Assandri, G., Bogliani, G., Pedrini, P. & Brambilla, M. 2018: Beautiful agricultural landscapes promote cultural ecosystem services and biodiversity conservation. — Agriculture, Ecosystems and Environment 256: 200–210.

Boyd, C., Punt, A. E., Weimerskirch, H. & Bertrand, S. 2014: Movement models provide insights into variation in the foraging effort of central place foragers. — Ecological Modelling 286: 13–25.

Brambilla, M., Pedrini, P., Rolando, A. & Chamberlain, D.E. 2016: Climate change will increase the potential conflict between skiing and high-elevation bird species in the Alps. — Journal of Biogeography 43: 2299–2309.

Brambilla, M., Cortesi, M., Capelli, F., Chamberlain, D., Pedrini, P. & Rubolini, D. 2017a: Foraging habitat selection by Alpine White-winged Snowfinches *Montifringilla nivalis* during the nestling rearing period. — Journal of Ornithology 158: 277–286.

Brambilla, M., Caprio, E., Assandri, G., Scridel, D., Bassi, E., Bionda, R., Celada, C., Falco, R., Bogliani, G., Pedrini, P., Rolando, A. & Chamberlain, D. 2017b: A spatially explicit definition of conservation priorities according to population resistance and resilience, species importance and level of threat in a changing climate. — Diversity and Distributions 23: 727–738.

Brambilla, M., Resano-Mayor, J., Scridel, D., Anderle, M., Bogliani, G., Braunisch, V., Capelli, F., Cortesi, M., Horrenberger, N., Pedrini, P., Sangalli, B., Chamberlain, D., Arlettaz, R. & Rubolini, D. 2018a: Past and future impact of climate change on foraging habitat suitability in a high-alpine bird species: Management options to buffer against global warming effects. — Biological Conservation 221: 209–218.

Brambilla, M., Capelli, F., Anderle, M., Forti, A., Bazzanella, M., Masiero, G., Bogliani, G., Partel, P., Pedrini, P., Pedrotti, L. & Scridel, D. 2018b: Landscape-associated differences in fine-scale habitat selection modulate the potential impact of climate change on White-winged Snowfinch *Montifringilla nivalis*. — Bird Study 65: 525–532.

Camfield, A.F. & Martin, K. 2009: The influence of ambient temperature on horned lark incubation behaviour in an alpine environment. — Behaviour 146: 1615–1633.

Cecere, J.G., Bond S., Podofillini, S., Imperio, S., Griggio, M., Fulco, E., Curcio, A., Ménard, D., Mellone, U., Saino, N., Serra, L., Sarà, M. & Rubolini, D. 2018: Spatial segregation of home ranges between neighbouring colonies in a diurnal raptor. — Scientific Reports 8: 11762.

Collins, P.M., Halsey, L.G., Arnould, J.P.Y., Shaw, P.J.A., Dodd, S. & Green, J.A. 2016: Energetic consequences of time-activity budgets for a breeding seabird. — Journal of Zoology 300: 153–162.

Cramp, S. & Perrins, C.M. 1994: Handbook of the Birds of Europe, the Middle East, and North Africa: The Birds of the Western Palearctic. Volume VIII: Crows to Finches. — Oxford University Press, Oxford

Cresswell, J.E., Osborne, J.L. & Goulson, D. 2000: An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. — Ecological Entomology 25: 249–255.

Danchin, É, Cézilly, F. & Giraldeau, L.-A. 2008: Behavioural Ecology. — Oxford University Press, Oxford.

Dunn, J.C., Morris, A.J. & Grice, P.V. 2017: Post-fledging habitat selection in a rapidly declining farmland bird, the European Turtle Dove *Streptopelia turtur*. — Bird Conservation International 27: 45–57.

Elliott, S.E. 2009: Subalpine Bumble Bee Foraging Distances and Densities in Relation to Flower Availability. — Environmental Entomology 38: 748–756.

Evans, J.C., Votier, S.C. & Dall, S.R.X. 2016: Information use in colonial living. — Biological Reviews 91: 658–672.

Furness, R.W. & Bryant, D.M. 1996: Effect of wind on field metabolic rates of breeding northern fulmars. — Ecology 77: 1181–1188.

Gobbi, M., Ballarin, F., Brambilla, M., Compostella, C., Isaia, M., Losapio, G., Maffioletti, C., Seppi, R., Tampucci, D. & Caccianiga, M. 2017: Life in harsh environments: carabid and spider trait types and functional diversity on a debris-covered glacier and along its foreland. — Ecological Entomology 42: 838–848.

Grémillet, D. 1997: Catch per unit effort, foraging efficiency, and parental investment in breeding great cormorants (*Phalacrocorax carbo carbo*). — ICES Journal of Marine Sciences 54: 635–644.

Grieco, F. 2002: Time constraint on food choice in provisioning blue tits, *Parus caeruleus*: The relationship between feeding rate and prey size. — Animal Behaviour 64: 517–526.

Hemberger, J. & Gratton, C. 2018: Floral resource pulse decreases bumble bee foraging trip duration in central Wisconsin agroecosystem. — Ecological Entomology 43: 447–457.

Jedlikowski, J., Chibowski, P., Karasek, T. & Brambilla, M. 2016: Multi-scale habitat selection in highly territorial bird species: Exploring the contribution of nest,

territory and landscape levels to site choice in breeding rallids (Aves: Rallidae). — Acta Oecologica 73: 10–20.

Klein, G., Vitasse, Y., Rixen, C., Marty, C. & Rebetez, M. 2016: Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snowmelt more than to later snow onset. — Climatic Change 139: 637–649.

Liang, D., Gao, G., Pagani-Núñez, E., Pang, H., Liu, Y., Luo, X. & Robinson, S.K. 2018: Incubation behaviour of a high-altitude species: the Fire-tailed Sunbird *Aethopyga ignicauda*. — Bird Study 65: 261–265.

Lu, X., Ke, D. H., Zeng, X.H. & Yu, T.L. 2009: Reproductive ecology of two sympatric Tibetan snowfinch species at the edge of their altitudinal range: Response to more stressful environments. — Journal of Arid Environments 73: 1103–1108.

Martin, K. & Wiebe, K. L. 2004: Coping mechanisms of alpine and arctic breeding birds: extreme weather and limitations to reproductive resilience. — Integrative and Comparative Biology 44: 177–185.

Muscio, G., Pellegrini, G., Solari, M., Tomaselli, M., Vanin, S. & Zanetti, A. 2005: Ambienti nivali. La vita in un ambiente estremo. — Ministero dell'Ambiente e della Tutela del Territorio, Museo Friulano di Storia Naturale, Comune di Udine.

Neteler, M., Bowman, M. H., Landa, M. & Metz, M. 2012: GRASS GIS: A multi-purpose open source GIS. — Environmental Modelling Software 31: 124–130.

Resano-Mayor, J., Korner-Nievergelt, F., Vignali, S., Horrenberger, N., Barras, A.G., Braunisch, V., Pernollet, C.A. & Arlettaz, R. 2019: Snow cover phenology is the main driver of foraging habitat selection for a high-alpine passerine during breeding: implications for species persistence in the face of climate change. — Biodiversity and Conservation: 1–17.

Scridel, D., Brambilla, M., Martin, K., Lehikoinen, A., Iemma, A., Matteo, A., Jähnig, S., Caprio, E., Bogliani, G., Pedrini, P., Rolando, A., Arlettaz, R. & Chamberlain, D. 2018: A review and meta-analysis of the effects of climate change on Holarctic mountain and upland bird populations. — Ibis 160: 489–515.

Strinella, E., Ricci, F. & Vianale, P. 2007: Uso dell'habitat nel Fringuello alpino (*Montifringilla nivalis*) in periodo riproduttivo in un'area sub-antropizzata: Campo Imperatore (Gran Sasso-Abruzzo). — Alula 14: 107–114.

Weimerskirch, H., Louzao, M., De Grissac, S. & Delord, K. 2012: Changes in wind pattern alter albatross distribution and life-history traits. — Science 335: 211–214.

Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. 2006: Foraging trip duration of bumblebees in relation to landscape-wide resource availability. — Ecological Entomology 31: 389–394.