Articles

Impact of spatial variation of a crucial prey, the molecricket, on hoopoe territory occupancy and reproduction

Nicolas Guillod, Raphaël Arlettaz and Alain Jacot

N. Guillod (nguillod@gmx.ch), R. Arlettaz and A. Jacot, Inst. of Ecology and Evolution, Division of Conservation Biology, Univ. of Bern, Bern, Switzerland. RA and AJ also at: Swiss Ornithological Inst., Valais Field Station, Sion, Switzerland.

Direct benefits accrued from securing a territory of sufficient quality are important determinants of individual fitness and population persistence. Food supply is one of the main factors of animal territory quality, with spatial and temporal variation in prey availability largely dictating reproductive output and thus population dynamics. In a Swiss hoopoe population, molecrickets *Gryllotalpa gryllotalpa*, the most profitable prey locally, can constitute most of the food biomass delivered to chicks by parents. We first investigated the impact of molecricket prey on hoopoes' fitness-related traits by quantifying the spatial variation in the food allocation pattern of both male and female parents to chicks across the whole population range; and second, analysed the impact of this prey on current reproduction and, using a 11 yr dataset, on the temporal occupancy rate of each territory. We found considerable but spatially repeatable variation, over the years, of molecricket biomass in the diet provisioned to chicks. This spatial heterogeneity in chicks' diet composition was mirrored both in the history of territory occupancy (2002–2012) and in current reproductive success (2012). Territories with a greater biomass of molecrickets in chicks' diet produced more fledglings in better body condition. Yet, these effects on current reproduction were exclusively demonstrated for male parents, corroborating that paternal provisioning patterns play a predominant role in hoopoe reproductive success. This study demonstrates how a single, very profitable prey species might affect spatial variation in territory settlement and individual reproductive success in a regionally endangered bird species, with potential consequences for its population dynamics and persistence.

Variation in food distribution and, especially, availability are critical factors influencing the reproductive performance of animal species (Martin 1987). Food availability varies in time and space, with selection favouring individuals responding to this environmental uncertainty by choosing high-quality territories and by timing their reproduction with peaks in prey abundance (Van Noordwijk et al. 1995, Arlettaz et al. 2000, Both et al. 2006). Thus, prey is hardly ever available at discretion, meaning that intraspecific competition forces some individuals to settle and breed in suboptimal habitats. This generally results in a despotic distribution of phenotypes across the landscape (Tschumi et al. 2014), which is mirrored in the reproductive output (Sergio and Newton 2003, Tremblay et al. 2003, Tschumi et al. 2014). Spatial variation in territory settlement and foraging ground use by a predatory species can hence largely be influenced by the habitat associations, population dynamics and phenology of the prey itself.

In birds, prey availability, along with nest site quality (Williams et al. 1991), is likely to play the most crucial role for population persistence. In blue tits *Cyanistes caeruleus*, for instance, a comparison across different breeding habitat types revealed that caterpillar abundance is the main determinant of traits related to reproduction, such as egg laying date, clutch size, chick growth and nestling survival (Perrins 1965, Tremblay et al. 2003). Even within a single habitat, such as xeric Mediterranean farmland, the local availability of molecricket prey has been shown to determine the onset of breeding in lesser kestrels *Falco naumanni* (Catry et al. 2012). In the hoopoe *Upupa epops*, another bird species that specializes on molecrickets in central European farmland, molecrickets may similarly play a predominant role in a chicks' diet and affect reproductive success (Fournier and Arlettaz 2001, Arlettaz et al. 2010a). General prey availability and in some cases even the availability of a single prey species may thus govern reproductive success, translating into variation in individual fitness and ultimately, the persistence of a bird population, which is key for conservation management.

Prey availability, which is abundance modified by accessibility from the perspective of the predator, remains difficult to measure in the field. Indeed, several studies have shown that prey accessibility, and not prey abundance, is often of superior importance for effective foraging, as demonstrated for terrestrially foraging insectivorous farmland birds (Martinez et al. 2010, Schaub et al. 2010, Weisshaupt et al. 2011, Tagmann-Ioset et al. 2012). Quantifying the prey provisioned to offspring indirectly allows the estimation of

prey availability within a territory during the breeding season, this although chicks' diet might slightly differ from that of adults, as it is likely to be optimised in response to the high selective pressures that operate during reproduction (Britschgi et al. 2006).

In this study we investigated the direct impact of molecrickets on various fitness-related traits in a Swiss hoopoe population. Firstly, applying an individual-based approach we studied the relationship between the biomass of molecrickets provisioned by male and female hoopoe parents to their chicks, i.e. molecricket availability, on current reproductive success and the probability to invest in second broods. Secondly, using a landscape approach, we investigated the link between molecricket 'availability' and the frequency at which a given nest box, i.e. territory, has been successfully occupied over eleven consecutive years (Sergio and Newton 2003). This approach represents a new attempt to directly link territory occupancy and territory holder's reproductive performance to molecricket availability, what previous studies were only able to infer indirectly from proxies of territory quality (Tschumi et al. 2014, Hoffmann et al. 2015). Such a dual approach should provide new insights into the mechanisms at play both in this unique predator–prey system and in hoopoe population dynamics, delivering information relevant to the management of this regionally endangered bird species.

Methods

Study area and species

The study was carried out in 2011 and 2012 (April to August) on the plain of the upper Rhône valley, in the south-western Swiss Alps (Valais, Switzerland; 46°07′N, 07°08′N) between Vernayaz and Sierre. The whole study area has an extension of roughly 70 km² and is characterized by high-intensity agriculture, dominated by fruit tree plantations and vegetable crops. The hoopoe is a migratory, presently endangered bird species in Switzerland (Bächler et al. 2010), which needs patches of bare soil on its feeding grounds for accessing their mostly underground-dwelling prey (Tagmann-Ioset et al. 2012). In the past, the Swiss population was much larger and occupied a much wider range, but its strongholds have always been in Valais (Arlettaz et al. 2010b). The Valais population itself reached very low levels in the 1980s, which elicited a targeted research project (Fournier and Arlettaz 2001) that identified a lack of suitable breeding sites close to the foraging grounds on the plain as a critical factor. Hundreds of nest boxes were therefore installed in agricultural sheds and buildings since 1999, which led to a dramatic increase of the population of this secondary cavity breeder within a few years only (Arlettaz et al. 2010b). The whole population has been monitored continuously since then, with comprehensive information about nest box occupancy, breeding parameters (clutch size, number of hatchlings and fledglings) and morphometric traits (body mass, tarsus length, measured at day 15–18 after hatching). More precisely, starting in April, all nest boxes were checked every second week. Occupied nest boxes were controlled about every second day through the entrance hole with a small mirror fixed on a flexible stick,

coupled to a light bulb. We recorded clutch size, hatching date, number of nestlings and fledglings. All fledglings were ringed between day 15 and 18 after hatching. Adults were captured and measured (body mass tarsus length) no earlier than 4 d after hatching of the nestlings, either with mist-nets or clap-traps.

Parental food provisioning

Sex-specific parental food provisioning behaviour was recorded at days 11–15 after hatching of the oldest chick, which corresponds to the time when the female stops brooding the young and helps the male in provisioning prey to offspring (Arlettaz et al. 2010a). In order to identify adult birds on the video footage, each individual was captured prior to filming at the nest and marked with a unique combination of three plastic colour bands and a numbered metal ring. Food delivery was filmed during 24 h either inside (infrared sensitive black and white, platin camera 8.47 mm, Conrad, Germany) or outside the nest box (colour platin camera 3.6 mm, Conrad, Germany). Each camera was connected to a solid-state recorder (Lupus AEON-MDVR, Landau, Germany) and powered by two 6 V car batteries. To accustom the feeding parents to the filming gear, cameras were installed one day prior to the filming day. In 2012 we monitored prey provisioning at 97 broods in 78 nest boxes, including second broods. We already had data about parental food provisioning from previous years at the same nest box locations. Of three nest boxes we had feeding data from three years (2002, 2011 and 2012), of 29 nest boxes we had recordings of two years (11 nest boxes in 2002 and 2012; 18 nest boxes in 2011 and 2012) (Arlettaz et al. 2010a and unpubl.). A comparison of these former data with the newly collected data allowed a quantification of the spatio-temporal consistency (i.e. repeatability) of chick diet composition within a given territory over the years.

Analysis of video footage

The 97 broods were video-monitored during an entire 24-h cycle, except 4 broods that could be filmed for 7–10 h only. This resulted in 2345 h of video footage, totalling 10 557 feeding events. The videos were analysed at $16 \times$ speed (VideoLan 1996, École Centrale Paris, France). For each feeding event, we recorded a) which parent (male/female) was feeding, b) the prey type fed (species as far as possible), and its size, and c) daytime. To estimate delivered prey biomass we distinguished three size categories with corresponding approximately estimated biomass from previous studies (Arlettaz et al. 1997, 2010a): large (adult) molecrickets (average dry biomass of 0.68 g), medium molecrickets (0.46 g) and small molecrickets (0.36 g). For large Lepidoptera larvae we also distinguished three biomass categories: large (0.1 g), medium (0.08 g) and small (0.06 g) larvae. To small, unidentified prey (3.35% of all prey items) we also assigned a dry biomass of 0.06 g while to medium unknown prey (1.3%) we assigned a weight of 0.36 g, the latter being equivalent to the dry biomass of small-sized molecrickets. When presenting the importance of molecrickets on hoopoes' fitness-related traits we use the term molecricket 'availability' to strengthen the fact that

the effectively delivered molecricket biomass is not only mediated through their abundance, but also through their accessibility. Molecricket 'availability' therefore corresponds to molecricket biomass delivered by parents.

Statistical analyses

In a first step, we calculated, referring to Lessells and Boag (1987), the repeatability over time of the spatial molecricket biomass delivered to chicks at a given nest box, i.e. territory (for details see above, n = 32) during entire days in 2002 (Arlettaz et al. 2010a), 2011 and 2012. This way we obtained a proxy of the temporal consistency of the amount of delivered biomass of molecrickets to a specific nest box.

All statistical analyses were performed with R, ver. 3.0.2 (R Development Core Team). When analysing the diel feeding pattern of adults we used generalized linear mixed models with the biomass of provisioned molecrickets per hour as dependent variable, the sex of the parent and daytime (in hourly units) as covariates and the pair id as random factor. When analysing the relationship between morphological measurements of parents (tarsus length, body mass) on the amount of provisioned molecricket biomass we used general linear models with a gaussian error distribution for each sex separately.

Reproductive output was measured in terms of clutch size, hatching and fledging success, as well as total number of fledglings per brood. For hatching and fledging success, we ran generalized linear models (function 'glm', Venables and Ripley 2002) with a binomial error distribution (hatched vs clutch-hatched; fledged vs hatched-fledged), provisioned molecricket biomass and date as covariates and nest box as random factor. Clutch size and the number of fledglings per brood were analyzed with general linear mixed models with a gaussian error distribution, provisioned molecricket biomass and date as covariates and nest box as random factor. The probability of performing a second brood in a given territory in relation to molecricket 'availability' was analyzed with a generalized linear model with binomial error distribution. The relationship between nestling body mass, structural size (i.e. tarsus length) in relation to provisioned prey was also analysed using general linear mixed models (function 'glmmPQL', Venables and Ripley 2002) with provisioned molecricket biomass and date as fixed factors and brood as a random effect.

In a further step, using the same statistical approaches as described above, we analysed the effect of molecrickets on hatching/fledging success and on chick body mass and tarsus size while controlling for brood size. This analysis reflects the residual importance of provisioned molecricket biomass on breeding performance given chick number.

We assessed the relationship between the amount of provisioned molecricket biomass (from dietary surveys in 2012) and territory occupancy rate (from 2002 through to 2012, i.e. 11 yr of data), first with sexes grouped, and then with sexes separated. Territory occupancy rate was obtained from the number of times over 11 yr a nest box was occupied (including second broods; Arlettaz et al. 2010a) out of the 93 nestboxes for which video footage was collected in 2012. A nestbox could thus have been occupied theoretically up to 22 times (actually observed range: 1–18). This data was

analysed by performing generalized linear models (function 'glm', Venables and Ripley 2002) with a binomial error distribution (occupied vs total-occupied) and molecricket availability and sex as fixed factors.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.c5h4p> (Guillod et al. 2016).

Results

Spatio-temporal repeatability of diet composition

Molecrickets represented 38.2% of prey item frequency but as much as 76.7% of overall delivered prey biomass. 52% of prey items were caterpillars and various insect larvae, the remaining 9.8% consisting of gryllidae, aranaeidea, earth worms, coleopterans, lizards and unknown prey (the latter making up 4.65% of frequency). There was a significant spatial repeatability ($r = 0.34$, $p = 0.014$) in the estimated molecricket biomass delivered to chicks over the years (video footage obtained from the same nest box in 2002, 2011 and 2012).

Chick provisioning patterns

Male and females showed a peak in feeding activity one to two hours after onset of the day with decreasing feeding activity toward the evening ($time^2 = -0.01 \pm 0.01$, $t_{3001} = -4.60$, $p < 0.001$). Although males fed less often than females (-0.89 ± 0.33, $t_{3000} = -2.70$, $p = 0.006$), there was no sex-specific temporal feeding pattern over the day ($time^2 \times sex$: 0.01 ± 0.01, $t_{3000} = 0.64$, $p = 0.51$).

When focussing on molecrickets, we see that males fed more biomass than females (0.04 ± 0.004, $t_{3935} = 11.35$, $p < 0.001$). This is due to males bringing more medium 4.09 ± 1.28, $z = 3.17$, $p = 0.02$) and large molecrickets (9.41 ± 1.14, $z = 8.24$, $p < 0.001$) compared to females. The amount of provisioned molecricket biomass was independent of parental tarsus sizes (males: 0.01 ± 0.01, $z = 0.76$, $p = 0.44$; females: 0.01 ± 0.01, $z = 0.3$, $p = 0.76$) and parental body mass (males: -0.09 ± 0.10, $z = -0.09$, $p = 0.36$; females: -0.05 ± 0.08, $z = -0.63$, $p = 0.52$).

Effect of provisioned molecricket biomass on current reproductive success

Breeding pairs that fed a greater absolute biomass of molecrickets showed a tendency to lay larger clutches (0.02 ± 0.01, $z = 1.82$, $p = 0.062$; date: -0.03 ± 0.01, $z = -5.54$, $p < 0.001$) and to have a greater number of offspring (0.05 ± 0.01, $z = 3.95$, $p = 0.0017$; date: -0.02 ± 0.01, $z = -3.17$, $p = 0.0072$). This pattern is best explained through pairs feeding higher amounts of molecrickets having a greater hatching (0.02 ± 0.01, $z = 2.93$, $p = 0.0115$; date: -0.004 ± 0.004, $z = -1.12$, $p = 0.27$) and fledging success (0.02 ± 0.01, $z = 2.97$, $p = 0.0108$; date: -0.003 ± 0.004, $z = -0.62$, $p = 0.54$). Nest boxes where a greater biomass of molecrickets was provisioned also had a higher probability of having a second brood (0.03 ± 0.01 $z = 5.69$, $p < 0.001$; date: -0.01 ± 0.01, $z = -4.80$, $p = 0.63$).
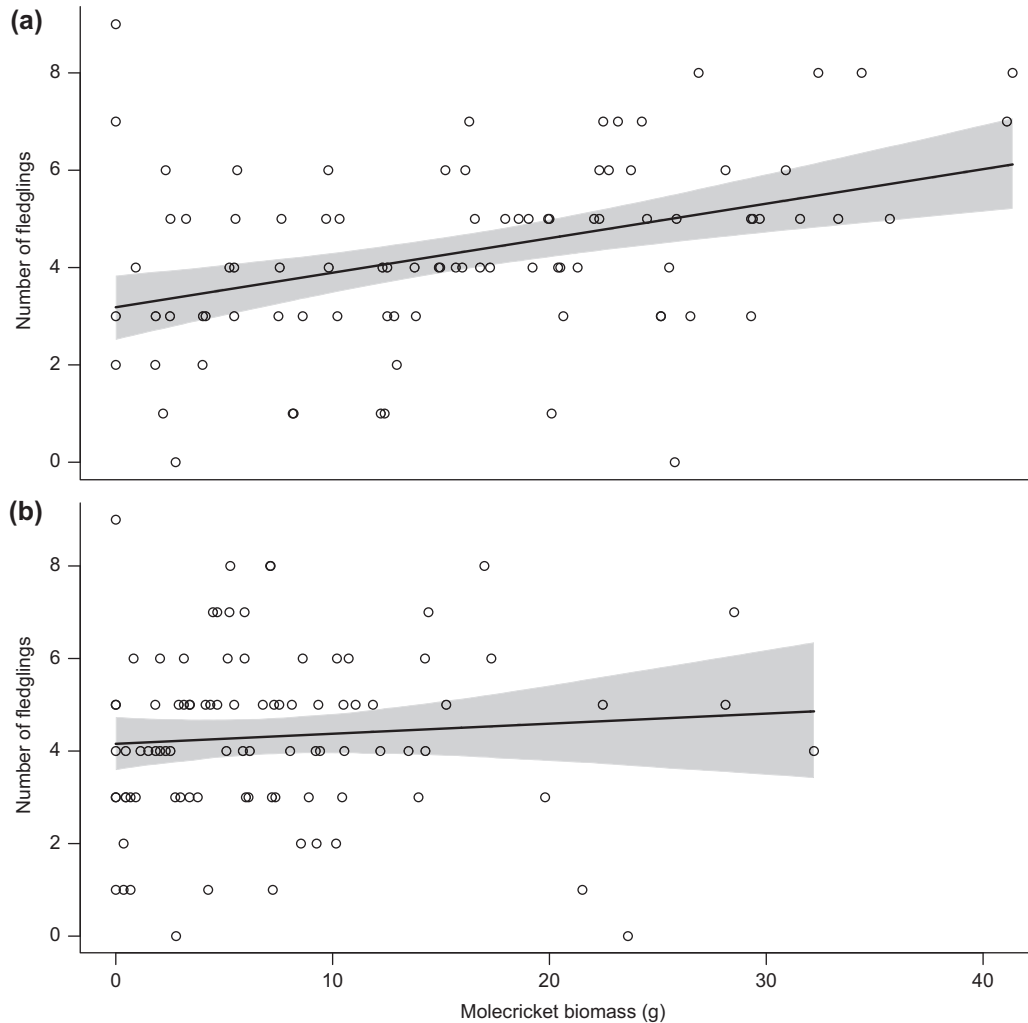
Figure 1. Relationship between the number of fledglings per nest site (nest box, n = 93 and the absolute molecricket biomass (in g, estimated dry weight) fed to chicks by (a) males (p < 0.001) and (b) females (p = 0.51). Shown in grey are the 95% CrI (credible intervals). Notice the larger contribution of molecrickets by male than female parents.

Considering the sexes separately, we found a significant positive relationship between the amount of molecrickets provisioned to offspring and clutch size in females (0.05 ± 0.02, $z = 2.62$, $p = 0.02$; date: -0.03 ± 0.01, $z = -5.77$, $p < 0.001$), but not in males (0.01 ± 0.01, $z = 0.61$, $p = 0.55$; date: -0.03 ± 0.01, $z = -5.29$, $p < 0.001$). In contrast, there was a positive relationship between number of fledglings and the biomass of molecrickets males provisioned to the chicks (0.07 ± 0.01, $z = 4.81$, $p = 0.0003$; date: -0.02 ± 0.01, $z = -2.96$, $p = 0.01$; Fig. 1a), while no such relationship was found in females (0.02 ± 0.02, $z = 0.64$, $p = 0.52$; date: -2.41 ± 0.01, $z = -3.12$, $p < 0.01$; Fig. 1b). Males that fed a greater biomass of molecrickets increased their reproductive success by having a greater hatching success (0.02 ± 0.01, $z = 2.86$, $p = 0.01$; date: -0.01 ± 0.01, $z = -0.94$, $p = 0.36$) and fledging success (0.04 ± 0.01, $z = 4.49$, $p = 0.0006$; date: -0.01 ± 0.01, $z = -0.28$, $p = 0.77$), while no such effect was found in females (hatching success: 0.01 ± 0.01, $z = 0.89$, $p = 0.38$; date: -0.01 ± 0.01, $z = -1.2$, $p = 0.25$; fledging success: -0.02 ± 0.01, $z = -0.51$, $p = 0.61$; date: -0.01 ± 0.01, $z = -0.68$, $p = 0.5$).

The probability to have a second brood depended on the biomass of provisioned molecrickets in males (0.04 ± 0.01, $z = 5.12$, $p < 0.001$; date: -0.01 ± 0.01, $z = -0.016$, $p = 0.98$) but not in females (0.01 ± 0.01, $z = 0.027$, $p = 0.97$; date: -0.01 ± 0.01, $z = -0.50$, $p = 0.63$).

The total amount of provisioned molecricket biomass affected chick body mass (0.12 ± 0.05, $t_{325} = 2.46$, $p = 0.01$; date: -0.03 ± 0.03, $t_{88} = -1.06$, $p = 0.30$), while no such effect was found on structural size, i.e. tarsus length (0.01 ± 0.01, $t_{743} = 0.69$, $p = 0.48$; date: 0.01 ± 0.01, $t_{88} = 0.69$, $p = 0.14$). When analyzing the two sexes separately, we found a positive effect of provisioned molecrickets on chick body mass in male feeding patterns (0.15 ± 0.06, $t_{325} = 2.33$, $p < 0.02$; date: -0.03 ± 0.03, $t_{88} = -0.94$, $p = 0.34$; Fig. 2a,), while no such effect was found in females (0.12 ± 0.1, $t_{325} = 1.17$, $p = 0.24$; date: -0.03 ± 0.03, $t_{88} = -1.02$, $p = 0.30$; Fig. 2b).

In a second step we analysed the amount of provisioned molecricket biomass by controlling for chick number. While hatching success and tarsus length were unaffected by the residual amount of provisioned molecrickets, we found
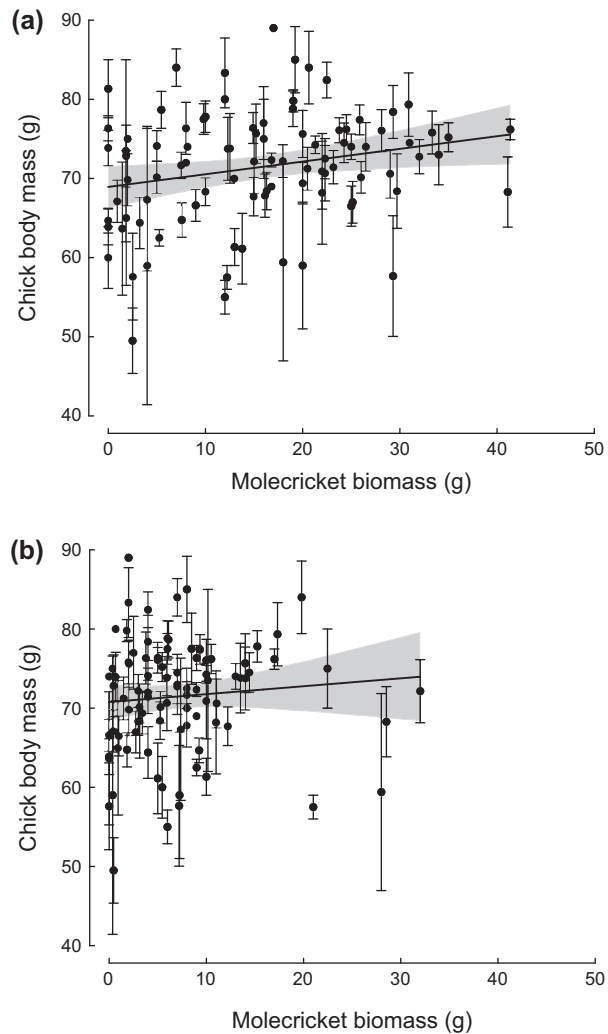
Figure 2. Relationship between absolute molecricket biomass (in g, estimated dry weight) fed to chicks by (a) males (p = 0.02) and (b) females (p = 0.24) in relation to mean (± SE) chick body mass per nest (n = 93). Shown in grey are the 95% CrI (credible intervals). Notice the larger contribution of molecrickets by male than female parents.

significant relationships with fledging success and body mass (Table 1). Interestingly, the residual amount of provisioned molecrickets by males positively affected chick body mass and fledging rate (p = 0.08) and while there was a negative effect of female provisioning behaviour on fledging success.

Effects of molecricket 'availability' on territory occupancy rate

Territory occupancy rate was affected by molecricket 'availability' (estimate ± SE = 0.024 ± 0.003, z = 6.99, p < 0.001): territories where greater biomasses of molecrickets were provisioned to chicks in 2012, had a higher occupancy rate between 2002 and 2012. This relationship is not due merely to the realization of second broods in a given territory: when restricting the analysis to first broods only, occupancy rate was still positively affected by the amount of provisioned molecricket biomass (0.024 ± 0.003, z = 6.39, p < 0.001). When parents were considered separately,

territory occupancy rate was affected by molecricket biomass for both sexes, where males (0.03 ± 0.004, z = 6.77, p < 0.001, Fig. 3a) showed a stronger relationship than females (0.01 ± 0.006, z = 2.97, p = 0.03, Fig. 3b).

Discussion

This study demonstrates and confirms previous indications that a single, locally extremely profitable prey species, the molecricket, can drive reproductive performance in a hoopoe population (Fournier and Arlettaz 2001, Arlettaz et al. 2010a). It also provides strong functional evidence for the despotic distribution of phenotypes observed among territory holders (Tschumi et al. 2014). It furthermore demonstrates that molecricket 'availability', indirectly evaluated from its contribution to chicks' diet, is spatially consistent over the years, boosting reproductive success. Finally, this study indicates that territory occupancy within- and between years is primarily driven by molecricket availability, revealing what is the main determinant of territory occupancy and quality (Tschumi et al. 2014).

The amount of provisioned molecrickets varied dramatically across the whole study area, ranging from 14% in suboptimal habitat to 100% in prey hotspots. This corroborates the findings by Arlettaz et al. (2010a) who found an average 93% biomass of molecrickets in chicks' diet in 26 broods during the early recolonisation phase, i.e. when only the most suitable habitat had been recolonised. The wide range of spatial molecricket 'availabilities' throughout the study area was in fact a prerequisite for testing the effects of the selective pressure that a single prey can exert on breeding birds in terms of territory settlement and reproductive success. This study establishes for the first time that molecricket 'availability' is the major drive of habitat selection (Tagmann-Ioset et al. 2012) and territory settlement (Bötsch et al. 2012, Tschumi et al. 2014) in our hoopoe population, demonstrating a posteriori its instrumental role in determining both territory quality, which had so far only been assessed indirectly via territory occupancy (Tschumi et al. 2014) and reproductive performance (Hoffmann et al. 2015). Territory selection in hoopoes is thus a non-random process, where hoopoes have the ability to perceive spatial heterogeneity in molecricket occurrence, abundance and/or accessibility, which is depicted by early arriving individuals being in better condition and systematically settling in superior territories (Tschumi et al. 2014), a pattern observed in other species as well (Village 1985, Kokko 1999).

Phenotypic traits expressing higher hierarchical status as well as superior territory quality estimated from its temporal occupancy (Tschumi et al. 2014, Hoffmann et al. 2015) correlate with greater molecricket occurrence in chicks' diet, hence translating into a higher reproductive success. Larger clutch sizes in molecricket-rich areas might either stem from the genetic background of adults, i.e. their intrinsic quality (Ortego et al. 2007, García-Navas et al. 2009, Wetzel et al. 2012), or reflect enhanced environmental conditions (Przybylo et al. 2001), but these two factors cannot easily be disentangled. The fact that nestlings growing in molecricket-rich territories became heavier, while their tarsus length remained unaffected, suggests a greater role of environmental

Table 1. Effects of chick number, provisioned molecricket biomass and date on hatching- and fledging success, chick body mass and chick tarsus length. For each response variable we analysed the effect of provisioned molecricket of both sexes together (total), and male and female separately.

Response variable		Predictor variable	Estimate ± SE	Test statistic	p
Hatching success	total	Intercept	−7149 ± 3981	1.80	0.07
		chick number	0.28 ± 0.04	7.76	<0.001
		molecricket biomass	−0.0003 ± 0.003	−0.09	0.92
		date	0.004 ± 0.002	1.80	0.08
	males	Intercept	−4386 ± 8154	−0.53	0.59
		chick number	0.28 ± 0.067	4.00	<0.001
		molecricket biomass	0.008 ± 0.01	0.84	0.41
		date	0.002 ± 0.004	0.53	0.6
	females	Intercept	−5797 ± 8123	−0.67	0.51
		chick number	0.3 ± 0.06	5.00	<0.001
		molecricket biomass	−0.004 ± 0.01	−0.31	0.76
		date	0.003 ± 0.004	0.71	0.48
Fledging success	total	Intercept	−9132 ± 4005	−2.28	0.025
		chick number	0.43 ± 0.03	10.99	<0.001
		molecricket biomass	0.003 ± 0.004	0.93	0.35
		date	0.005 ± 0.002	2.28	0.02
	males	Intercept	−14278 ± 7832	−1.91	0.06
		chick number	0.37 ± 0.07	5.86	<0.001
		molecricket biomass	0.01 ± 0.009	1.93	0.08
		date	0.007 ± 0.004	1.91	0.07
	females	Intercept	−18429 ± 7244	−2.54	0.01
		chick number	0.47 ± 0.06	8.13	<0.001
		molecricket biomass	−0.03 ± 0.01	−2.99	0.01
		date	0.009 ± 0.004	2.54	0.02
Chick body mass	total	Intercept	108351 ± 71888	1.51	0.13
		chick number	−0.64 ± 0.55	−1.17	0.24
		molecricket biomass	0.13 ± 0.05	2.32	<0.02
		date	−0.05 ± 0.04	−1.51	0.14
	males	Intercept	96008 ± 71703	1.34	0.18
		chick number	−0.57 ± 0.55	−1.04	0.30
		molecricket biomass	0.16 ± 0.07	2.34	0.01
		date	−0.05 ± 0.04	−1.34	0.18
	females	Intercept	73843 ± 73374	1.01	0.32
		chick number	−0.11 ± 0.53	−0.21	0.83
		molecricket biomass	0.14 ± 0.11	1.24	0.22
		date	−0.04 ± 0.04	−1.01	0.32
Chick tarsus length	total	Intercept	−14614 ± 7056	−2.01	0.04
		chick number	0.09 ± 0.05	1.59	0.11
		molecricket biomass	0.002 ± 0.005	0.43	0.66
		date	0.007 ± 0.004	2.07	0.04
	males	Intercept	−16201 ± 7025	−2.31	0.02
		chick number	0.11 ± 0.05	2.01	0.04
		molecricket biomass	−0.004 ± 0.007	0.62	0.53
		date	0.008 ± 0.003	2.31	0.02
	females	Intercept	−14593 ± 6976	−2.01	0.04
		chick number	0.09 ± 0.05	1.77	0.08
		molecricket biomass	0.009 ± 0.01	0.89	0.37
		date	0.007 ± 0.003	2.09	0.04

factors than parental genetic background (Smith and Dhondt 1980). In addition, nestlings in molecricket-rich territories showed a higher hatching and fledging rate, which can be directly related to the amount of food provisioned to chicks (Arlettaz et al 2010a). Finally, from the perspective of the adults, we found that parents breeding in molecricket-rich territories had a higher probability to produce a second brood within the same season – a trait that can be indistinctly assigned to either individual or environmental quality, if not a combination of the two (Senar et al. 2002). The recent study by Hoffmann et al. (2015) reaches similar conclusions without being able to conclusively disentangle between these two factors. Overall, we conclude that the availability of a single prey, molecrickets, is a major component of an individual's current reproductive success in the hoopoe and may be of equal importance or even outweigh variation in individual characteristics related to a non-random settlement among territories (Tschumi et al. 2014).

The positive effect of provisioned molecricket biomass was less evident after controlling for brood size. This is not totally surprising given that pairs in molecricket-rich territories lay larger clutches, hence increasing their current reproductive
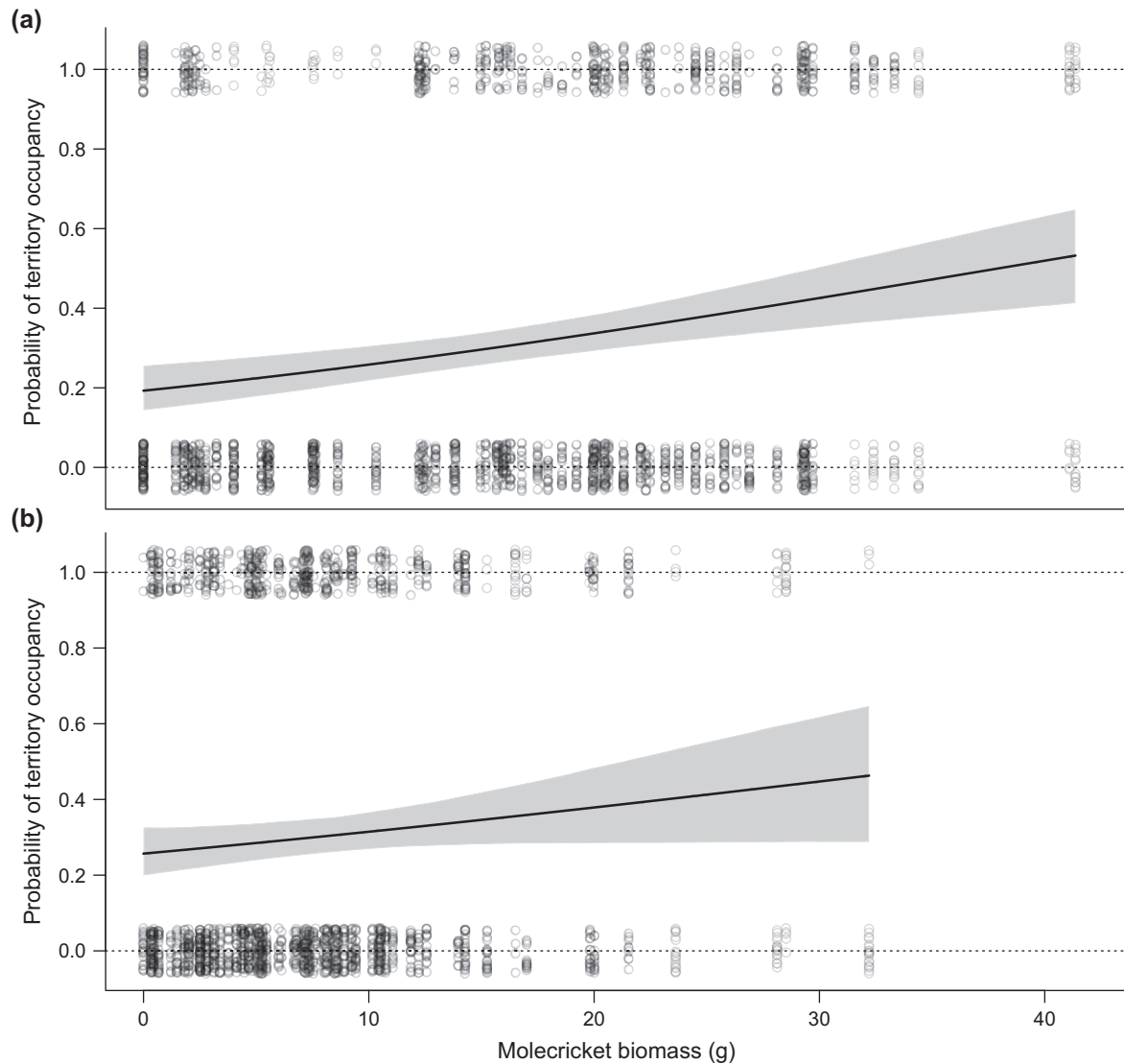
Figure 3. Relationship (n = 93) between territory occupancy rate and the absolute biomass of molecrickets in g, estimated dry weight) provisioned to chicks by (a) male (p < 0.001) and (b) female parents (p = 0.03). Shown in grey are the 95% CrI (credible intervals) while the raw data have been arbitrarily jittered around 0 (= not occupied) and 1 (= occupied) to enhance clarity.

success by producing more fledglings instead of investing more in single offspring. Trading-off offspring quantity for offspring quality is not expected when all fledglings reach an optimal body condition, i.e. when any extra-investment in chicks is unlikely to increase their future fitness (Lack 1947).

Molecricket-rich territories were occupied more often than molecricket-poor territories. As shown for other species (Crick et al. 1993), individual fitness in the hoopoe, as a multiple breeder depends not only on the number of fledglings produced in a single brood but also on the number of successful breeding attempts both during one season and during an individual's lifespan (Hoffmann et al. 2015). Given the apparent spatio-temporal consistency in trophic conditions (this study) and that adults tend to be loyal to their high-quality territories in the same and consecutive breeding seasons we expect significant inter-individual fitness differences across the study area that can largely be assigned to a single prey species (Gavin and Bollinger

1988, Wiklund 1996, Forero et al. 1999, Schaub and von Hirschheydt 2009).

Interestingly, all significant effects of molecricket availability on current reproductive success related exclusively to the feeding patterns of the male, confirming their crucial role for pairs' breeding performance (Tschumi et al. 2014). This indicates different sex-specific foraging strategies, i.e. the exploitation of slightly different trophic niches between the genders, with males allocating greater quantities of larger molecrickets, i.e. overall more molecricket biomass to nestlings than females (Arlettaz et al. 2010a, this study). Such a sex-specific differentiation of the foraging niche has been shown in a closely related species, the green woodhoopoe (Radford and Du Plessis 2003) and in blue tits where it could be related to sex-specific constraints on the time budget where females have to invest in other activities such as brooding or nest sanitation (Banbura et al. 2001).

We conclude that patterns of habitat selection and territory settlement in the hoopoe are driven by the local 'availability'

of a single prey, molecricket, its staple food source locally. This constitutes a major advance: so far only proxies of habitat quality had been used (Tschumi et al. 2014) where the study failed to demonstrate a link between molecrickets and reproductive success. This link is now clearer although still evoked indirectly via spatial variation in chicks' diet. Future studies will have to better appraise how this crucial resource can be maintained – especially in fruit tree plantations, the dominant foraging habitat in the study area – and whether alternative prey can be promoted in foraging grounds that offer sufficient accessibility to ground-foraging hoopoes (Tagmann-Ioset et al. 2012). A strong dependency on a single prey type represents a risk for endangered species, especially so in simplified, intensively used landscapes that mostly offer a much impoverished invertebrate food supply. More efforts must be consented for increasing prey offer via adequate habitat management if one wants to keep rare emblematic biodiversity in our future landscapes.

References

Arlettaz, R., Perrin, N. and Hausser, J. 1997. Trophic resource partitioning and competition between the two sibling bat species *Myotis myotis* and *Myotis blythii*. – J. Anim. Ecol. 66: 897–911.

Arlettaz, R., Fournier, J. and Zbinden, N. 2000. Evolution démographique (1979–1998) d'une population témoin de Huppe Fasciée *Upupa epops* en Valais et stratégie de conservation ciblée. – Nos Oiseaux 47: 19–27.

Arlettaz, R., Schaad, M., Reichlin, T. S. and Schaub, M. 2010a. Impact of weather and climate variation on hoopoe reproductive ecology and population growth. – J. Ornithol. 151: 889–899.

Arlettaz, R., Schaub, M., Fournier, J., Reichlin, T. S., Sierro, A., Watson, J. E. M. and Braunisch, V. 2010b. From publication to public actions: when conservation biologists bridge the gap between research and implentation. – BioScience 60: 835–842.

Bächler, E., Hahn, S., Schaub, M., Arlettaz, R., Jenni, L., Fox, J. W., Afanasyev, V. and Liechti, F. 2010. Year-round tracking of small trans-Saharan migrants using light-level geolocators. – PLoS One 5: e9566.

Banbura, J., Perret, P., Blondel, J., Sauvages, A. N. N. E., Galan, M. J. and Lambrechts, M. M. 2001. Sex differences in parental care in a Corsican blue tit *Parus caeruleus* population. – Ardea 89: 517–526.

Both, C., Bouwhuis, S., Lessells, C. M. and Visser, M. E. 2006. Climate change and population declines in a long-distance migratory bird. – Nature 441: 81–83.

Bötsch, Y., Arlettaz, R. and Schaub, M. 2012. Breeding dispersal of Eurasian hoopoes (*Upupa epops*) within and between years in relation to reproductive success, sex, and age. – Auk 129: 283–295.

Britschgi, A., Spaar, R. and Arlettaz, R. 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the whinchat *Saxicola rubetra*: lessons for overall Alpine meadowland management. – Biol. Conserv. 130: 193–205.

Catry, I., Franco, A. M. A. and Sutherland, W. J. 2012. Landscape and weather determinants of prey availability: implications for the lesser kestrel *Falco naumanni*. – Ibis 154: 111–123.

Crick, H. Q. P., Gibbons, D. W. and Magrath, R. D. 1993. Seasonal changes in clutch size in British birds. – J. Anim. Ecol. 62: 263–273.

Forero, M. G., Donazar, J. B. and Fernando, H. 1999. Causes and consequences of territory change and breeding dispersal distance in the black kite. – Ecology 80: 1298–1310.

Fournier, J. and Arlettaz, R. 2001. Food provision to nestlings in the hoopoe *Upupa epops*: implications for the conservation of a small endangered population in the Swiss Alps. – Ibis 143: 2–10.

García-Navas, V., Ortego, J. and Sanz, J. J. 2009. Heterozygosity based assortative mating in blue tits (*Cyanistes caeruleus*): implications for the evolution of mate choice. – Proc. R. Soc. B 276: 2931–2940.

Gavin, T. A. and Bollinger, E. K. 1988. Reproductive correlates of breeding-site fidelity in bobolinks (*Dolichonyx oryzivorus*). – Ecology 69: 96–103.

Guillod, N., Arlettaz, R. and Jacot, A. 2016. Data from: Impact of spatial variation of a crucial prey, the molecricket, on hoopoe territory occupancy and reproduction. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.c5h4p>.

Hoffmann, J., Postma, E. and Schaub, M. 2015. Factors influencing double brooding in Eurasian hoopoes *Upupa epops*. – Ibis 157: 17–30.

Kokko, H. 1999. Competition for early arrival in migratory birds. – J. Anim. Ecol. 68: 940–950.

Lack, D. 1947. The significance of clutch size 1. Intraspecific variation. – Ibis 89: 302–352.

Lessells, C. M. and Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. – Auk 104: 116–121.

Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspecrive. – Annu. Rev. Ecol. Syst. 18: 453–487.

Martinez, N., Jenni, L., Wyss, E. and Zbinden, N. 2010. Habitat structure versus food abundance: the importance of sparse vegetation for the common redstart *Phoenicurus phoenicurus*. – J. Ornithol. 151: 297–307.

Ortego, J., Calabuig, G., Cordero, P. J. and Aparicio, J. M. 2007. Egg production and individual genetic diversity in lesser kestrels. – Mol. Ecol. 16: 2383–2392.

Perrins, C. 1965. Population fluctuations and clutch-size in the great tit, *Parus major* L. – J. Anim. Ecol. 34: 601–647.

Przybylo, R., Wiggins, D. A. and Merilä, J. 2001. Breeding success in blue tits: good territories or good parents? – J. Avian Biol. 32: 214–218.

Radford, A. N. and Du Plessis, M. A. 2003. Bill dimorphism and foraging niche partitioning in the green woodhoopoe. – J. Anim. Ecol. 72: 258–269.

Schaub, M. and von Hirschheydt, J. 2009. Effect of current reproduction on apparent survival, breeding dispersal, and future reproduction in barn swallows assessed by multistate capture–recapture models. – J. Anim. Ecol. 78: 625–635.

Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M. L., Reichlin, T. S., Abadi, F., Zbinden, N., Jenni, L. and Arlettaz, R. 2010. Patches of bare ground as a staple commodity for declining ground-foraging insectivorous farmland birds. – PLoS One 5: e13115.

Senar, J. C., Figuerola, J. and Pascual, J. 2002. Brighter yellow blue tits make better parents. – Proc. R. Soc. B 269: 257–261.

Sergio, F. and Newton, I. 2003. Occupancy as a measure of territory quality. – J. Anim. Ecol. 72: 857–865.

Smith, J. N. M. and Dhondt, A. A. 1980. Experimental confirmation of heritable morphological variation in a natural population of song sparrows. – Evolution 34: 1155–1158.

Tagmann-Ioset, A., Schaub, M., Reichlin, T. S., Weisshaupt, N. and Arlettaz, R. 2012. Bare ground as a crucial habitat feature for a rare terrestrially foraging farmland bird of central Europe. – Acta Oecol. 39: 25–32.

Tremblay, I., Thomas, D. W., Lambrechts, M. M., Blondel, J. and Perret, P. 2003. Variation in blue tit breeding performance across gradients in habitat richness. – Ecology 84: 3033–3043.

Tschumi, M., Schaub, M. and Arlettaz, R. 2014. Territory occupancy and parental quality as proxies for spatial prioritization of conservation areas. – PLoS One 9: e97679.

Van Noordwijk, A. J., McCleery, R. H. and Perrins, C. M. 1995. Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. – J. Anim. Ecol. 64: 451–458.

Venables, W. N. and Ripley, B. D. 2002. Modern applied statistics with S. – Springer.

Village, A. 1985. Spring arrival times and assortative mating of kestrels in south Scotland. – J. Anim. Ecol. 54: 857–868.

Weisshaupt, N., Arlettaz, R., Reichlin, T. S., Tagmann-Ioset, A. and Schaub, M. 2011. Habitat selection by foraging wrynecks *Jynx torquilla* during the breeding season: identifying the optimal habitat profile. – Bird Study 58: 111–119.

Wetzel, D. P., Stewart, I. R. and Westneat, D. F. 2012. Heterozygosity predicts clutch and egg size but not plasticity in a house sparrow population with no evidence of inbreeding. – Mol. Ecol. 21: 406–420.

Wiklund, C. G. 1996. Determinants of dispersal in breeding merlins (*Falco columbarius*). – Ecology 77: 1920–1927.

Williams, J. B., Du Plessis, M. A. and Siegfried, W. R. 1991. Green woodhoopoes (*Phoeniculus purpureus*) and obligate cavity roosting provide a test of the thermoregulatory insufficiency hypothesis. – Auk 108: 285–293.