Short-Term Foraging Costs and Long-Term Fueling Rates in Central-Place Foraging Swans Revealed by Giving-Up Exploitation Times

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ABSTRACT: Foragers tend to exploit patches to a lesser extent farther away from their central place. This has been interpreted as a response to increased risk of predation or increased metabolic costs of prey delivery. Here we show that migratory Bewick's swans (*Cygnus columbianus bewickii*), though not incurring greater predation risks farther out or delivering food to a central place, also feed for shorter periods at patches farther away from their roost. Predictions from an energy budget model suggest that increasing metabolic travel costs per se are responsible. Establishing the relation between intake rate and exploitation time enabled us to express giving-up exploitation times as quitting harvest rates (QHRs). This revealed that net QHRs were not different from observed long-term net intake rates, a sign that the birds were maximizing their long-term net intake rate. This study is unique because giving-up decisions were measured at the individual level, metabolic and predation costs were assessed simultaneously, the relation with harvest rate was made explicit, and finally, short-term giving-up decisions were related to long-term net intake rates. We discuss and conceptualize the implications of metabolic traveling costs for carrying-capacity predictions by bridging the gap between optimal-foraging theory and optimal-migration theory.

Keywords: carrying capacity, central-place foraging (CPF), depletion, giving-up density (GUD), marginal value theorem (MVT), optimal migration.

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Threshold intake rates at which foragers give up a patch have been the focus of many studies since Eric Charnov proposed the marginal value theorem (MVT; Charnov 1976). Such quitting harvest rates (QHRs) can be informative to ecologists for various reasons, providing knowledge on patch assessment abilities (Valone and Brown 1989; van Gils et al. 2003), habitat suitability (Piersma et al. 1995; Olsson et al. 1999), mechanisms of competition and coexistence (Shochat et al. 2004), carrying capacity (Gill et al. 2001; van Gils et al. 2004), fitness prospects, and metabolic and predation costs of foraging as perceived by the foragers themselves (Olsson et al. 2002; Stenberg and Persson 2006).

The MVT states that in order to maximize long-term intake rate, a forager should give up a patch when the marginal intake rate in the patch drops to the long-term intake rate for the habitat. Brown (1988) generalized the concept of the MVT by including costs associated with foraging in a given patch. His model predicts QHR to increase with metabolic and predation costs of foraging. Recently, Brown and Kotler (2004) reviewed the overwhelming evidence that foragers take account of predation costs. Fewer studies have investigated the effects of the metabolic costs of foraging, which, for example, may include thermostatic costs (Kotler et al. 1993; Meyer and Valone 1999), harvesting costs (Nolet et al. 2001, 2006a), or digestion costs (Shochat et al. 2004). In case a forager frequently returns to a patch from a central place, such as a nest, a burrow, or a roost, the metabolic costs required while traveling between the central place and the patch can also be considered as foraging costs associated with that particular patch (provided that only this patch and not multiple patches are visited on a single trip). Note that this type of foraging belongs to the realm of central-place foraging (CPF; Orians and Pearson 1979), which in birds has often been studied in the context of parents delivering food to their young (e.g., Wilson et al. 2005) but is here considered for nonbreeding, migratory birds that rest at a central roost each night during stopover.

Figure 1: When to give up a patch that is visited on multiple days from a central place? *A*, While feeding in a patch, gross energy intake accumulates at a decelerating rate. Cumulative metabolic costs increase stepwise because of daily trips commuting from and to the central place. Costs are plotted for two patches: one far away (high daily travel costs) and one nearby (low costs). For simplicity, we ignored other metabolic costs and the time cost of traveling. Net-rate-maximizing foragers should give up each patch when the marginal net rate of energy intake in the patch drops to the average net rate of energy intake along the flyway. For simplicity, we assumed this average net rate to be 0 (but depending on costs of resting and traveling between stopovers, it could be higher or lower than that). In that case, the optimal time in the patch is found where the slope of the gross intake curve equals the (overall) slope of the cumulative metabolic cost line. Here this results in an optimal time of 7 days in the faraway patch and 25 days in the nearby patch. Note that this policy does lead to a positive net energy balance over the full foraging period (inclusive of commuting), even though the long-term net intake rate equals 0 in this habitat because of other costs not plotted here (roosting and traveling between stopovers). *B*, An alternative way of depicting the same problem: plotting derivatives of the curves in *A*. Optimal exploitation time is where the declining gross intake rate line crosses the horizontal metabolic rate line. *C*, Thus, with an increasing distance between patch and central place, metabolic rate and thus optimal gross quitting harvest rate increase (note that we assumed that traveling back and forth one unit of distance costs one metabolic unit). *D*, Accordingly, optimal giving-up time declines with increasing distance.

Imagine that such birds trade off migration speed against risk of predation along a migratory flyway that consists of stopovers (e.g., Ydenberg et al. 2002). Note that migration speed is here defined as the overall speed of migration, not only regarding the actual time to fly between subsequent stopovers but also including the time required to fuel at stopovers (Alerstam and Lindström 1990). Trading off migration speed against risk of predation boils down to maximizing migration speed when we assume a constant risk of predation everywhere and for all activities (Olsson and Brown 2006). Since maxi-

mizing migration speed is similar to minimizing fueling time, it is equivalent to maximizing long-term net intake rate (Alerstam and Lindström 1990; Hedenström and Ålerstam 1998). Let us further assume that each stopover harbors one roost, which is surrounded by a (finite) number of patches. There are two patch types: patches located near the roost and patches located far from the roost (fig. 1). We further assume that an individual bird visits only a single patch on a given day and flies back to the roost each night. On the next day, it may continue to exploit the same patch (a patch is large enough to support multiple

birds for multiple days), start exploiting another patch, or continue its migration. The two patch types available are similar with respect to initial prey density and searching efficiency (hence, only one intake curve is drawn in fig. 1A). Since search within patches is random and the food is nonrenewable, the marginal intake rate declines with exploitation time in the patch (fig. 1A, 1B). Following from the MVT, a patch should be given up when the marginal net intake rate in the patch drops to the long-term net intake rate expected along the flyway. The marginal net intake rate in the patch equals the marginal gross intake rate minus the marginal metabolic costs involved in exploiting that patch. Since the timescale of the bird's giving-up decision is in terms of days rather than seconds, these marginal metabolic costs include, among other metabolic costs, the travel costs needed to commute from and to the roost. Note that this opposes the more general foraging scenario where an animal is able to visit multiple patches within a single foraging bout, in which case the marginal costs and benefits of foraging are evaluated at the timescale of seconds (e.g., Brown et al. 1992; Bowers et al. 1993; van Gils et al. 2003). However, for the case considered here, patches located near the roost are cheaper to exploit and should thus be given up at lower gross intake rates than patches located farther out (fig. 1B, 1C), meaning that the optimal time spent in a patch should decline with its distance to the roost (fig. 1D). Note that this seems opposite to most textbook examples of the MVT, where time in a patch increases with travel distance (e.g., Stephens and Krebs 1986); the reason for this apparent difference is that those examples compare different habitats (each with its own long-term intake rate), while here we vary travel time within a single habitat.

Many studies have documented foragers that exploited patches near the central place more thoroughly than patches farther out. This has been explained either by predation costs increasing with distance to the refuge (Lima 1988; Brown et al. 1992; Cassini and Galante 1992; Bowers et al. 1993; Kotler et al. 1993, 1999; Brown and Morgan 1995; but see Bakker et al. 2005) or by an increase in the metabolic (and time) costs of delivering food to the central place (Andersson 1978, 1981; Kacelnik 1984; Fryxell 1992). Here we show that the foraging decisions in a large, nonbreeding migrant, the Bewick's swan (*Cygnus columbianus bewickii*), roosting at a central place each night, are governed by metabolic costs during travel (between roost and foraging sites) and by predation costs during feeding.

Our focus is on a surrogate of QHR, namely, cumulative exploitation time expressed in bird-days, a measure often used in studies of carrying capacity of stopovers sites for migratory birds (Sutherland and Anderson 1993; Goss-Custard et al. 2003; van Gils et al. 2004). Relating this

proxy to distance to the roost, overlaid by predictions based on net rate maximization, enables us to estimate the relative importance of metabolic travel costs. The importance of predation costs is assessed by relating (this proxy of) QHR to distance to roads (cf. Gill et al. 1996) because the main source of disturbance in our densely populated study area is due to humans rather than to (other) predators. Note that most studies on giving-up decisions investigate another surrogate of QHR, namely, the amount of prey remaining in the patch, that is, the giving-up density (GUD; Brown and Kotler 2004). In order to translate our proxy of QHR into real QHRs, we quantified for a number of fields the relation between cumulative exploitation time and intake rate, a critical test that is often missing in studies using GUD as a proxy (Price and Correll 2001). Moreover, and again in contrast to most GUD studies, we express our giving-up decisions at the individual level. Usually GUDs are measured at the population level, which may lead to underestimates of GUD and QHR as artificial food patches are fed on last by those individuals accepting the lowest GUD. Finally, a nice feature that studies on Bewick's swans and other large waterfowl enable is the ability to actually measure long-term net intake rates by scoring abdominal profiles over time (Bowler 1994; Madsen and Klaassen 2006). This allowed us to perform the most definitive test of the MVT: comparing (surrogates of) marginal net intake rates upon patch departure with average long-term net intake rates (at the average level of the population).

Methods

During three consecutive winters (2003/2004, 2004/2005, and 2005/2006), from late October to early February, we almost daily counted the number of Bewick's swans per arable field throughout Wieringermeer, an agricultural area (225 km²) in the northwestern Netherlands (52°48'N, 05°05'E). On these fields, Bewick's swans feed on the remains of sugar beets spilled during harvesting by farmers. Each flock encountered was scanned by telescope for individuals with a coded leg or neck ring. Approximately one out of each 160 Bewick's swans is individually marked by a coded leg ring or neck collar (J. A. van Gils, personal observation), which enabled us to express giving-up decisions at the individual level. Using ArcView GIS (ESRI 1996), we estimated for each occupied field the distance to the swans' main roost at Normerven (in the north of the study area), the distance to the nearest road, and the surface area.

Dropping Rate R

In studies on herbivorous waterfowl, dropping rates of feces are often used to estimate gross intake rates, as direct observations on intake rates are difficult to obtain because of high bite rates and/or variable bite sizes (Prop and Black 1998; Prop and Quinn 2003). We used these rates too and estimated them by applying the so-called hourly-block method (Bédard and Gauthier 1986). This consists of counting the number of droppings produced by a haphazardly selected single individual until losing contact with this bird, after which a new focal individual is selected. The procedure is continued until a full hour has passed. Observations were made on haphazardly selected flocks from a car at a distance of 70–200 m using a 60 × telescope (Meade Instruments, Irvine, CA). Data were collected in the first two winters only. We excluded observations that started before 11 a.m. because defecation starts 2–3 h after the initiation of eating (J. A. van Gils and A. Gyimesi, unpublished data), leading to 37 observations analyzed. We tested for diminishing returns, a critical assumption of MVT, by analyzing dropping rates R (h^{-1}) as a function of the cumulative number T of bird-days that a field had been exploited (bird-hours, assuming that 1 bird-day contains 10.3 bird-h; Nolet et al. 2002). In order to do so, dropping rates were $\log_e$ transformed. Analyses were performed in the following hierarchical linear model (HLM), using the MIX procedure in SYSTAT 10 (Systat 2000):

$$\log_e R = \log_e (ax_0)_i - aT + \varepsilon, \quad (1)$$

which yields parameter estimates for searching efficiency a (h^{-1}) and initial food density x_0 (here expressed as the total number of droppings that would have been produced if a field were to be exploited fully); ε is a normally distributed error. This random-search model (Olsson et al. 2001) ignores handling time, which is justified since in swans it is very short relative to the time spent searching (J. A. van Gils, personal observation). Note that we estimated field-specific intercepts (indicated by i), correcting for possible variation between fields in initial food density. Parameter estimates a and x_0 were used to translate giving-up exploitation times T_{quit} into quitting dropping rates R_{quit} in case of the observations (next section) and vice versa in case of the predictions (after next section).

Observed Giving-Up Bird-Days T_{quit}

For each field, we calculated per day the cumulative number of swans that had visited the field so far, yielding a measure of patch exploitation time T expressed in bird-days. This enabled us, for each individually marked bird, to translate its giving-up date per field into a number T_{quit}

of bird-days that a field had been exploited so far. Moreover, it enabled us to express the final number of swan-days upon which a field was fully abandoned by all birds (individually marked or not). Before analyzing these giving-up decisions as a function of distance to the roost (D_{roost}) and distance to the nearest road (D_{road}), we excluded fields that were plowed immediately after the last day that swans visited the field because in those cases plowing rather than depletion was the reason for swans to give up the field. Moreover, we excluded fields located at $D_{\text{roost}} > 13$ km, as swans visiting those fields usually roosted at other locations (J. A. van Gils, personal observation). Sixty-five fields were suitable for analysis and were visited by exactly 100 marked birds, leading to 382 giving-up decisions to be analyzed. (In 25 of these cases [7%], individuals revisited a field after they initially seemed to have abandoned it because another field was chosen in between. These revisits, however, were included in the analysis since it is the final giving-up decision by an individual on a given field that matters.) Because all fields were more or less similarly sized (mean $\pm$ SE surface of 7.8 ± 0.4 ha), for convenience we express our measures of foraging pressure per field rather than per square meter. Analyses were performed in the following HLM using the MIX procedure in SYSTAT 10 (Systat 2000):

$$R_{\text{quit}} = c_j + b_1 D_{\text{roost}} + b_2 D_{\text{road}} + \varepsilon. \quad (2)$$

Quitting dropping rate R_{quit} was calculated by filling in T_{quit} for T (in hours) in equation (1) (using parameter estimates a and x_0). Note that we estimated individual-specific intercepts (indicated by j), thereby taking account of possible distance-independent variation in R_{quit} between individuals. According to the MVT, this variation reflects individual differences in long-term net intake rate, assuming that metabolic rates during flight, foraging, and resting do not differ between individuals and that predation costs at the average patch and roost are similar (Olsson and Brown 2006).

*Predicted Giving-Up Bird-Days T_{quit}^**

Optimal giving-up exploitation times T_{quit}^* were predicted from hypothetical and observed long-term average daily fueling rates $\bar{F}$ (kJ day^{-1}) in the following way. The rate $\bar{F}$ is determined by time and energy lost to traveling between stopovers and the feeding policy at stopovers. With respect to feeding policy, assuming maximization of $\bar{F}$, birds in an MVT context should give up a field when their “instantaneous” fueling rate F (kJ day^{-1}) drops to $\bar{F}$:

$$F = \bar{F}. \quad (3)$$

Because the decision for which field to go to is made at the timescale of a day, the instantaneous fueling rate F is evaluated over the full day rather than over just seconds. It therefore equals daily metabolizable energy intake (DMEI; kJ day^{-1}) minus daily energy expenditure (DEE; kJ day^{-1} , including the flight costs to and from the roost):

$$F = \text{DMEI} - \text{DEE}. \quad (4)$$

So a field should be given up when

$$\text{DMEI} - \text{DEE} = \bar{F}. \quad (5)$$

DMEI is calculated as

$$\text{DMEI} = t_{\text{forage}} R \beta \frac{\alpha}{1 - \alpha}, \quad (6)$$

where R is dropping rate (h^{-1}), β is a dropping's energy content (21.25 kJ, based on 27 droppings collected in the 2003/2004 winter and 50 droppings collected in the 2005/2006 winter), and α is the assimilation efficiency on sugar beets (0.71, the average of the value used by Nolet et al. [2002] and our three measurements during the 2003/2004 winter).

DEE is calculated as

$$\text{DEE} = 3.6(t_{\text{forage}} m_{\text{forage}} + t_{\text{fly}} m_{\text{fly}} + t_{\text{rest}} m_{\text{rest}}), \quad (7)$$

where t_{forage} is daily time spent foraging (10.3 h; Nolet et al. 2002) at a metabolic rate m_{forage} (28.3 W; Nolet et al. 2002), t_{fly} is daily time spent flying ($2D_{\text{roost}}/v_{\text{fly}}$, expressing D_{roost} in kilometers and using a velocity v_{fly} of 46.2 km h^{-1} , as observed by Nolet et al. [2002] for short foraging flights) at a metabolic rate m_{fly} (1,116.5 W, derived from estimates made by Powell and Engelhardt [2000] for short foraging flights by tundra swans at the flight speed observed by Nolet et al. [2002], which takes into account an efficiency of 0.23 for converting fat into mechanical energy [cf. Powell and Engelhardt 2000]), and t_{rest} is daily time spent resting at the roost ($24 - t_{\text{forage}} - t_{\text{fly}}$) at a metabolic rate m_{rest} (22.2 W; Nolet et al. 2002).

Given equation (5), we can now rewrite equation (6), which solves for the optimal quitting dropping rate R_{quit}^* (h^{-1}) at an individual field,

$$R_{\text{quit}}^* = \frac{\text{DEE} + \bar{F}}{t_{\text{forage}} \beta [\alpha/(1 - \alpha)]}. \quad (8)$$

In order to explicitly include the variable of interest, D_{roost} , into equation (8), we can substitute for DEE, which yields

$$R_{\text{quit}}^* = \{3.6[t_{\text{forage}} m_{\text{forage}} + 2(D_{\text{roost}}/v_{\text{fly}})(m_{\text{fly}} - m_{\text{rest}}) + (24 - t_{\text{forage}}) m_{\text{rest}}] + \bar{F}\} / \{t_{\text{forage}} \beta [\alpha/(1 - \alpha)]\}, \quad (9)$$

which shows that R_{quit}^* increases with an increase in distance D_{roost} (because $m_{\text{fly}} > m_{\text{rest}}$).

According to the random search model (eq. [1]), and taking account of 10.3 h of foraging per day, (gross) R_{quit}^* is achieved after an optimal number of T_{quit}^* bird-days,

$$T_{\text{quit}}^* = \frac{\log_e [R_{\text{quit}}^* / (ax_0)]}{-10.3a}. \quad (10)$$

Long-Term Fueling Rate $\bar{F}$

Estimates of long-term net intake rates $\bar{F}$ were obtained at the individual level by tracking changes in abdominal profile indices (APIs) of six individually marked birds throughout the Netherlands during the final field season, 2005/2006. APIs relate strongly to an individual's body mass and fat storage (Madsen and Klaassen 2006). Using the indices specifically developed for Bewick's swans (Bowler 1994), we estimated an individual's API every 7.1 days (SE = 1.2 days) from December 22, 2005, to February 22, 2006 (see van Gils et al. 2007). We assumed that 1 API unit corresponds to 420 g of fat mass (Bowler 1994). Furthermore, we assumed that depositing 1 g of fat requires 40 kJ (contents) plus a biosynthesis cost of 0.33 kJ kJ^{-1} of tissue (Ricklefs 1974). To test whether this long-term fueling rate $\bar{F}$ (kJ day^{-1}) differed from the observed short-term fueling rate F at patch quitting, we expressed $\bar{F}$ in droppings h^{-1} (by dividing it by $t_{\text{forage}} \beta [\alpha/(1 - \alpha)]$) and calculated the so-called net quitting dropping rate $R_{\text{quit, net}}$, which equals (gross) R_{quit} minus the costs due to energy expenditure (DEE calculated as in eq. [7]):

$$R_{\text{quit, net}} = R_{\text{quit}} - \frac{\text{DEE}}{t_{\text{forage}} \beta [\alpha/(1 - \alpha)]}. \quad (11)$$

Results

Dropping Rate R

Dropping rate R declined as a function of time in the patch (fig. 2A; $P < .00001$; residual variance = 0.08; $N_{\text{level 2}} = 9$ fields; $N_{\text{level 1}} = 37$ observations). This demonstrates that, for a given field, the birds were experiencing diminishing returns, which supports the basic assumption of MVT. Parameter estimates $\pm$ SE yielded $x_0 = 203,395 \pm 24,665$ droppings field^{-1} and $a = 5.3 \times$

Figure 2: A, Dropping rate of feces R (h⁻¹) declines exponentially with time T spent in a patch (bird-days). B, T_{quit} , that is, cumulative time spent in each field upon giving up (bird-days), declines with distance to the roost (km). Circles and error bars give means $\pm$ SE for individually marked birds, while triangles give means for the last birds to abandon the field (marked or not). Gray curves and band give optimal giving-up times T_{quit}^* when long-term average fueling rate $\bar{F}$ equals 0 and 0.05 API units day⁻¹ (curves) and when it lies within the 95% confidence interval of the observed $\bar{F}$ (band).

$10^{-5} \pm 9.7 \times 10^{-6}$ h⁻¹. Note that the estimate for a translates into a searching efficiency of 4.1 m² h⁻¹ (given the average field surface area of 7.8 ha), which corresponds with an earlier estimate of 4 m² h⁻¹ for Bewick's swans foraging aquatically (Nolet et al. 2001).

Giving-Up Bird-Days T_{quit} and Quitting Dropping Rate R_{quit}

Giving-up exploitation times T_{quit} declined as a function of distance to the roost (fig. 2B), and thus quitting dropping rates R_{quit} increased with distance to the roost (fig. 3A; $P < .00001$; residual variance = 5.16; N level 2 =

100 individuals; N level 1 = 382 observations). Parameter estimate $\pm$ SE yielded slope $b_1 = 0.34 \pm 0.04$ h⁻¹ km⁻¹, which does not differ from the predicted value (eq. [9]) of 0.32 h⁻¹ km⁻¹ ($P > .5$). The rate R_{quit} decreased with distance to the road: $b_2 \pm$ SE = -2.23 ± 0.61 h⁻¹ km⁻¹ (fig. 4; $P < .0005$). Net quitting dropping rate $R_{quit, net}$ (mean $\pm$ SE = 1.36 ± 0.14 h⁻¹; $N = 100$ individuals), possibly reflecting long-term net intake rates, indeed did not differ from the observed long-term fueling rate $\bar{F} \pm$ SE of 0.024 ± 0.005 API units day⁻¹ (i.e., 0.98 ± 0.21 droppings h⁻¹; $N = 6$ individuals; fig. 3B; $P > .5$). As expected, T_{quit} and R_{quit} by the last (usually unmarked) birds

Figure 3: A, Quitting dropping rate R_{quit} (h⁻¹), calculated from T_{quit} (fig. 2B), increases with distance to the roost (km). Symbols, curves, and gray band have the same meaning as in figure 2B. B, Frequency distribution of each individual's net quitting dropping rate $R_{quit, net}$. This measure, which is the deviation of (gross) R_{quit} from the 0 line plotted in A, can be transformed into a quitting instantaneous daily fueling rate (upper axis). The gray band represents observed $\bar{F}$, as in A and figure 2B.

Figure 4: Quitting dropping rate R_{quit} (h^{-1} ; left axis) decreases and giving-up exploitation time T_{quit} (bird-days; right axis) increases with distance to the nearest road (km). For reasons of visual clarity, we have categorized distance into two groups (unlike in the statistical analysis). The line gives hierarchical linear model regression; box-and-whisker plots give mean (circle), median (line within box), interquartile range (box), and range (bars). Gray band represents observed $\bar{F}$, as in figures 2B and 3.

to abandon a field (triangles in figs. 2B, 3A) were significantly higher (349 bird-days, $P < .00001$, $t = 6.90$) and lower (-1.08 droppings h^{-1} , $P < .00001$, $t = -7.92$), respectively, than those of the average marked individual, which confirms the idea that GUDs are underestimated when studied at the population level instead of the individual level.

Discussion

With increasing distance to the roost, swans gave up fields after shorter flock exploitation times (i.e., T_{quit}), and thus at higher gross QHRs (i.e., R_{quit}). Modeling their energy budget based on a priori determined metabolic parameters suggests that metabolic foraging costs increased with distance. Furthermore, with decreasing distance to the nearest road, fields were given up at higher gross QHRs, presumably because of higher levels of human disturbance, reflecting an increase in cost of predation. Thus, the basic qualitative prediction of Brown's (1988) extension of the MVT has been met: gross QHRs increased with increasing foraging costs. Furthermore, in spite of the fact that disturbance led to variation between fields in the net QHR (i.e., $R_{\text{quit, net}}$), the average net QHRs at which fields were given up did not differ from observed long-term net intake rates $\bar{F}$. Thus, the basic quantitative prediction of the MVT has been met: (on average) patches were given up when the marginal net rate of capture F had dropped to the long-term net rate of capture $\bar{F}$ along the flyway. This

policy maximizes $\bar{F}$, which is in line with observations on Bewick's swans at an aquatic stopover site (Nolet et al. 2006b). How swans, and migratory birds in general, are able to estimate their own expected long-term rate of fueling $\bar{F}$, enabling them to make such rate-maximizing decisions, is still a mystery. Possibly, their best guess is based on their long-term fueling rate achieved so far, for which they may get an estimate by using hormonal information. There is evidence that leptin, a regulatory hormone produced by the adipose tissue, may play a key role (Löhmus et al. 2003; Kochan et al. 2006).

An alternative explanation for the observation that fields farther out were exploited to a lesser degree could be the idea that the swans, upon their arrival at the stopover site, started exploiting the fields nearest to their roost first (for reasons other than the maximization of their net intake rate), while progressively spreading out farther as the nearby fields got depleted. By the time the birds left the stopover to continue their migration, fields farther out would have been exploited to a lesser extent simply because the swans' annual routine forced them to continue their migration. However, this alternative idea is ruled out by an analysis showing that, for birds that visited multiple fields each winter, there was no correlation between a field's distance to the roost and the order in which it was exploited ($Z = 1.0$, $P > .3$; HLM including N level 2 = 69 birds, N level 1 = 77 bird $\times$ winter combinations, and 339 giving-up decisions). Moreover, this alternative idea does not predict the observed equalization of net QHRs across different distances.

In a comparable study, Alonso et al. (1995) found that common cranes (*Grus grus*) exploiting arable fields also showed an increase in gross QHR with distance to the roost. The authors explained this by suggesting that the cranes behaved as gross-rate maximizers that daily dwelled through different habitats, with the best habitat being farthest out. Because patch use theory on gross-rate maximization predicts gross QHR to increase with habitat quality, this assumption seemed to explain their results. However, we reiterate that gross intake rate can be maximized only if animals apply the same gross QHR throughout their entire home range. For some reason, the habitat may be better farther away from the roost, but with that habitat being only a part of the cranes' daily home range, it would be suboptimal (under gross-rate maximization) to abandon those fields at a higher gross QHR. In the light of our current study, we therefore suggest that the cranes likely behaved as net-rate maximizers in which the metabolic cost of traveling explains Alonso et al.'s (1995) findings.

As mentioned in the introduction to this article, in many other studies, an increase in gross QHR with an increase in distance to the refuge is explained by animals incurring

higher risk of predation farther away. This makes sense for small mammals making multiple short feeding trips per day from their burrow because for them the time exposed to an approaching predator increases with distance to the burrow (Kramer and Bonenfant 1997). However, in swans making a single long feeding trip per day, the chance to escape a predator is not at all related to the distance to the roost, since these large birds face only ground-dwelling predators and are therefore safe once airborne. In their case, risk of predation is more likely related to the potential distance to predators (mainly humans, in the case of swans wintering in the Netherlands), which explains the increase in QHR with a decrease in distance to the road. Red foxes (*Vulpes vulpes*) may occasionally kill Bewick's swans (Rees 2006), and therefore distance to cover alongside a field (for the fox to hide in) may additionally affect QHRs. In future studies, it may be interesting to explore individual differences in the cost of predation, which would be revealed by differences in the slope of (gross) QHR versus distance to roads (or cover): steeper slopes would be indicative of higher perceived predation costs. Such differences may arise because of individual differences in perceived risk of predation, in the marginal value of energy, or in fitness prospects (Olsson et al. 2002).

Elaborating further on differences between individuals: there is considerable interindividual variability in net QHR (fig. 3B). Following from the MVT, this should reflect individual differences in long-term fueling rates. Unfortunately, we cannot test this idea because we do not have data on API fueling rates of the individuals analyzed here (long-term fueling rates presented here were collected on individuals caught in Wieringermeer but resighted at other stopovers in the Netherlands). However, by compiling all resightings made throughout the entire Wieringermeer stopover, we do know each individual's total length of stay in this area. Migration theory based on the premise of time minimization (i.e., net-intake rate maximization) predicts that those individuals fueling fastest (both locally and along the flyway) should stay the shortest time at a given stopover site (Hedenström and Ålerstam 1997). Indeed, stopover times (mean $\pm$ SE = 13.9 ± 3.3 days) declined with net QHRs ($P < .05$; residual variance 0.14; N level 2 = 100 individuals, N level 1 = 116 observations [some birds were seen during multiple winters]). The fact that the slope of this relation appears to be less steep than -1 (i.e., $-0.8 \pm \text{SE} = 0.4$, when using log-transformed variables) also provides support for the net-rate maximization hypothesis, which predicts fuel loads upon migratory departure (i.e., stopover time $\times$ fueling rate) to increase with fueling rate (in spite of the shorter stopover times; Hedenström and Ålerstam 1997). However, -0.8 ± 0.4 does not differ significantly from -1 ($P > .5$), and we thus cannot rule out the idea that the birds de-

parted after they had gathered a fixed amount of fuel (cf. van Gils et al. 2007), which is predicted for migrants aiming to minimize the energetic costs of transport per unit distance (Hedenström and Ålerstam 1997).

Having gained insights into the threshold intake rates used by swans, we can now begin to understand the carrying capacity of our study area. Carrying capacity for migratory birds has often been expressed in terms of number of bird-days that an area is able to support (energetic or bird-day carrying capacity; Sutherland and Anderson 1993; Goss-Custard et al. 2003; van Gils et al. 2004; Nolet et al. 2006b). However, from a population ecological perspective, it is more relevant to use its classical demographic definition (Vandermeer and Goldberg 2003), which is the number of individuals that can be supported by an area. By melding optimal-patch use theory with optimal-migration theory, we may be able to arrive at a quantitative prediction of demographic carrying capacity for migratory birds (re)fueling at a stopover (conceptualized in fig. 5). First, by making use of MVT, one can predict from the observed average fueling rate $\bar{F}$ (0.024 API units day^{-1} in case of our swans) the optimal gross QHR, QHR^* , for each field (fig. 5A). Namely, through the daily energetic costs of commuting to and from a roost, a field's distance to the roost determines a bird's DEE. Under the premise of MVT, a bird should give up a field when the daily gross harvest rate minus the DEE equals its long-term fueling rate $\bar{F}$. Then, by making use of a bird's functional response, one can calculate the optimal giving-up exploitation time T_{quit}^* at which QHR^* is reached (fig. 5B; $T_{\text{quit}}^* = 686.1$ bird-days for the average field in Wieringermeer, weighted for the observed frequency distribution of D_{roost} ; note that T_{quit}^* does not differ from the observed mean $T_{\text{quit}} \pm \text{SE}$ of 793.0 ± 77.9 bird-days). Summing up T_{quit}^* for all fields at the stopover, one arrives at the predicted bird-day carrying capacity of the site: $\sum T_{\text{quit}}^*$ (82,330 bird-days for the entire Wieringermeer, which harbors ~ 300 sugar beet fields, of which only $\sim 40\%$ are suitable for exploitation because the rest are plowed immediately after harvest by the farmer; note that this prediction does not differ from the observed mean $\sum T_{\text{quit}} \pm \text{SE}$ of $86,233 \pm 8,054$ bird-days). Next, migration theory, assuming maximization of migration speed, predicts that an individual migrant should depart from its stopover when its instantaneous speed of migration has dropped to its expected overall speed of migration (fig. 5C; Ålerstam and Lindström 1990; Hedenström and Ålerstam 1997; using the same MVT principle as in patch use theory). Instantaneous speed of migration declines in the course of fueling because of the mass-dependent energetic cost of flight: the potential range that can be traveled obviously increases with an increase of the amount of fuel "on board"; however, this is a decelerating function because a heavier body means that a shorter distance can be covered per unit

Figure 5: How to predict demographic carrying capacity of a stopover site? A, The marginal value theorem in a nutshell: optimal foragers should give up a patch when their short-term net intake rate (gross harvest rate – energetic costs) equals their long-term net intake rate (i.e., fueling rate $\bar{F}$), that is, optimal quitting harvest rate $QHR^* = \bar{F} + \text{energetic costs}$. B, The QHR^* is reached after T time units of exploitation, that is, at an optimal giving-up exploitation time T_{quit}^* . C, Theory on time-minimizing migration predicts that individual migrants should depart from their stopover when their instantaneous migration speed (the slope of the decelerating curve) has declined to their expected overall migration speed (the slope of the straight line), that is, at T_{fuel}^* . D, Now, bird-day carrying capacity is the sum of T_{quit}^* for each patch at the stopover. Hence, demographic carrying capacity is bird-day carrying capacity divided by the average individual optimal stopover time T_{fuel}^* .

fuel. Using the observed overall speed of spring migration of 25.6 km day^{-1} (i.e., 3,200 km is covered during 125 days in spring; Beekman et al. 2002; note that migration speeds observed by Nolet [2006] were somewhat higher, 41.1 km day^{-1} on average; however these were not calculated across the entire flyway but from the next stopover in Germany onward) and the observed fueling rate, as mentioned above, we predicted an optimal stopover fueling time T_{fuel}^* of 9.8 days (see the appendix for more details on this prediction; note that this value does not differ from the observed mean $T_{fuel} \pm \text{SE}$ of 13.9 ± 3.3 days). Finally (fig. 5D), demographic carrying capacity can now be calculated as the bird-day carrying capacity divided by an individual's optimal stopover time: $\sum T_{quit}^* / T_{fuel}^*$. In the case considered here, we thus predict that 8,401 individuals make use of Wieringermeer each year, which is not different from the observed mean $\pm \text{SE}$ number of $8,005 \pm 1,577$ individuals

(estimated by dividing the number of marked individuals seen each winter, 45.7 ± 5.2 , by the annual average proportion of marked individuals in the local population, $6.1\% \pm 1.2\%$). These predictions (and observations) suggest that 25%–33% of the world population of Bewick's swans passes through our study area each year, making the area more important than suggested by previous estimates based on maximum number of birds counted per day (2% by Koffijberg et al. 1997; 5%–10% by Rademakers 2006).

In conclusion, the blend between migration theory (Alterstam and Hedenström 1998), on the one hand, and patch use theory (Charnov 1976; Brown 1988), on the other hand, may help us to mechanistically unravel the carrying capacity of stopovers along migratory flyways. This approach may help us understand and forecast population developments of long-distance migrants, which are cur-

rently under threat in a rapidly changing world (e.g., Both et al. 2006).

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APPENDIX

Predicting Optimal Fueling Time T_{fuel}^*

We used the following equation, provided by Alerstam and Lindström (1990) and based on mechanical-flight theory, in order to model potential flight range Y (km) as a function of fuel time T_{fuel} (days):

$$Y = c \left(1 - \frac{1}{\sqrt{1 + \bar{F}T_{\text{fuel}}}} \right), \quad (\text{A1})$$

where c is a proportionality constant (kilometers) and $\bar{F}$ is fueling rate, but now expressed as the daily increase in fuel mass relative to lean mass. Differentiating this equation with respect to T_{fuel} gives the decline in instantaneous migration speed (kilometers per day) as a function of T_{fuel} ,

$$\frac{dY}{dT_{\text{fuel}}} = \frac{c}{2} \bar{F} (1 + \bar{F}T_{\text{fuel}})^{-3/2}. \quad (\text{A2})$$

Because a time-minimizing migrant should depart from its stopover when its instantaneous migration speed has fallen to its expected overall migration speed S_{exp} (estimated at 25.6 km day⁻¹ by Beekman et al. 2002), the optimal fueling time equals

$$T_{\text{fuel}}^* = \frac{[(2S_{\text{exp}}/c\bar{F})]^{-2/3} - 1}{\bar{F}}. \quad (\text{A3})$$

Here, $\bar{F}$, in its relative expression, was calculated from the observed average increase of 0.024 API units day⁻¹, while assuming a fuel mass of 0.420 kg API unit⁻¹ (Bowler 1994)

and a lean mass of 5.6 kg (Beekman et al. 2002). The proportionality constant was calculated by assuming that a Bewick's swan can potentially cover 3,000 km when departing at its maximum relative fuel load f (fuel/lean mass) of 0.24 (Beekman et al. 2002). Because $f = \bar{F}T_{\text{fuel}}$, the proportionality constant in this case equals

$$\begin{aligned} c &= \frac{Y}{1 - (1/\sqrt{1 + f})} \\ &= \frac{3,000}{1 - (1/\sqrt{1 + 0.24})} = 29,419 \text{ km}. \end{aligned} \quad (\text{A4})$$

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