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Untying the knot

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Chapter 5

Beyond the information centre hypothesis

COMMUNAL ROOSTING FOR INFORMATION ON FOOD, PREDATORS, TRAVEL COMPANIONS AND MATES?

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SUMMARY   Communal roosting – the grouping of more than two individuals resting together – is common among animals, notably birds. The main functions of this complicated social behaviour are thought to be reduced costs of predation and thermoregulation, and increased foraging efficiency. One specific hypothesis is the Information Centre Hypothesis (ICH) which states that roosts act as information centres where individuals *actively* advertise and share foraging information such as the location of patchily distributed foods. Empirical studies in corvids have demonstrated behaviours consistent with the predictions of the ICH, but some of the assumptions in its original formulation have made its wide acceptance problematic. Here we propose to generalise the ICH in two ways: (1) dropping the assumption that information transfer must be active, and (2) adding the possibilities of information exchange on, for example, predation risk, travel companions and potential mates. A conceptual model, inspired by shorebirds arriving at roosts after foraging on cryptic prey, is proposed to illustrate how testable predictions can be generated. The conceptual model illustrates how roost arrival timing may convey inadvertent information on intake rate, prey density, forager state (i.e. digestive processing capacity) and food quality. Such information could be used by naïve or unsuccessful foragers to select with whom to leave the roost at the subsequent foraging opportunity and thus increase foraging success. We suggest that inadvertent information transfer, rather than active information exchange, predominates in communal roosts.

INTRODUCTION

Communal roosting occurs in taxa such as mammals (Lewis 1995), insects (Yackel Adams 1999) and arachnids (Grether and Donaldson 2007), but is best known from birds (Eiserer 1984). In this paper we focus on communally roosting birds and define a communal roost as a group of more than two individuals that come together to rest (Beauchamp 1999). The size of roosting groups varies from a few individuals as seen in house finches *Carpodacus mexicanus* (Dhondt et al. 2007), to roosts of several hundred-thousand individuals as in some songbirds and shorebirds (Black 1932, van de Kam et al. 2004, Winkler 2006). Within roosts, individuals can be highly site-faithful and consistently use the same resting spot (Eiserer 1984). In shorebirds, Charadrii, communal roosting sites can offer a degree of safety, if they are located in open areas with unobstructed views of their surroundings (Piersma et al. 1993a, Rogers et al. 2006, Rosa et al. 2006). In contrast, forest birds such as owls prefer concealed roosts in trees (Hayward and Garton 1984, Wijnandts 1984). Some communal roost locations can be used for many years. Some roosts of starlings *Sturnus vulgaris* have for instance existed for more than 180 years (Davis 1955). Despite extensive study and debate, the evolutionary origin of communal roosting remains unresolved (Danchin et al. 2008).

A classical way to view the evolution of communal roosting is by cost-benefit analyses. Costs associated with communal roosting can consist of increased exploitative and inter-ference competition (Grover 1997, Keddy 2001), increased likelihood of detection by predators (Page and Whitacre 1975, Eiserer 1984), and transmission of pathogens and parasites (Moore et al. 1988, Kulkarni and Heeb 2007, Buehler and Piersma 2008). Benefits include reductions in thermoregulation costs (Brenner 1965, Wiersma and Piersma 1994, Hatchwell et al. 2009), safety by numbers from predation, as well as increased predator detection (Lack 1968, Gadgil 1972, Krebs and Davies 1993, Krause and Ruxton 2002), and increased information on foraging opportunities (Ward and Zahavi 1973).

Contradicting the main viewpoint at that time – that the evolutionary origin of communal roosting was only related to safety from predators – Ward & Zahavi (1973) argued (1) that roosts and breeding colonies could act as information centres where individuals *actively* advertise and share information on the location of patchily distributed foods, and (2) that this advantage was the *primary* evolutionary origin of communal roosting. This became known as the Information Centre Hypothesis (ICH). However inspiring, the ICH has been surrounded by controversy and objection, in particular that information benefits were the primary origin of communal roosting (e.g., Richner and Danchin 2001). To date, several studies have shown that the use of social information can promote group living (Danchin and Wagner 1997, Danchin et al. 1998, Brown et al. 2000, Wagner et al. 2000, Dall 2002, Wagner and Danchin 2003, see Danchin et al. 2008). Nonetheless, the evolutionary origin of communal roosting remains obscure, probably because there is no *single* benefit which led to the evolution of communal roosting (Crook 1965, Beauchamp 1999). The debate on the evolutionary origin of communal

roosting has overshadowed the debate that communal roosts could serve as information centres. In this contribution we will focus on the information centre mechanism of communal roosting and the information benefits individuals could gain. *Information* is defined as "anything that reduces uncertainty and changes the state of the receiver in a potentially functional manner" (from Jablonka 2002, and see Danchin et al. 2004, Dall et al. 2005).

Empirical evidence for communal roosts as information centres is mostly lacking (Mock et al. 1988, Richner and Heeb 1995). Some argue that the ICH should be abandoned all together, because more parsimonious hypotheses are available (e.g., Richner and Heeb 1995, Danchin and Richner 2001) and the ICH does not describe an evolutionary stable strategy (ESS). The evolutionary maintenance of advertising foraging success to unrelated individuals can only be explained by reciprocal altruism, whereby individuals gain and lose in turn (Mock et al. 1988, Richner and Heeb 1995). This, however, is thought an unlikely condition for roosting birds, because roost composition is very dynamic (e.g., Conklin and Colwell 2008) and cheaters would be hard to identify and punish (Trivers 1971). There are several reasons, however, why communal roosts could function as information centres. Modelling studies have provided evidence that even in the presence of cheaters some individuals will always keep searching for new food patches as long as a 'finder's fee' exists (Barta and Giraldeau 2001). Additionally, Lachmann et al. (2000) showed that individuals living in groups have more information available and at lower costs, and that communal roosting can be an ESS if information cannot be hidden from roost mates. If information is inadvertent, aggregations could be maintained through information-sharing mechanisms and be evolutionarily stable. On the other hand, there are cases in which information is exclusive and where the sharing of information has a cost, e.g., active information transfer by displaying. In such cases, mechanisms must operate that enable the information provider to benefit from providing information (Danchin et al. 2008), as in the two strategy hypothesis (Weatherhead 1983), or the recruitment centre hypothesis (Richner and Heeb 1995) or through kin selection (e.g., Danchin et al. 2008).

More than thirty years after publication of the ICH, its validation remains unresolved and controversial. Now, advancements in the "ecology of information" and the emergence of an information framework (e.g., Danchin et al. 2004), allow for a reconsideration of the ICH. In the present attempt, we will first review recent empirical evidence for the ICH. Second, we will generalise the ICH. Finally, we will present a framework to guide future studies of information use at communal roosts, i.e. a conceptual model that allows for testable predictions.

EMPIRICAL SUPPORT

Since Ward & Zahavi (1973), many studies have examined the possibility of communal roosts acting as information centres, but usually fail to provide convincing evidence (see Ydenberg and Prins 1984, Mock et al. 1988, Richner and Heeb 1995). Generally, local

enhancement (e.g., foragers cueing in on individuals that are already foraging and visible from the roost) cannot be ruled out (Mock et al. 1988, Richner and Heeb 1995). Until recently, only two studies on breeding colonies found evidence consistent with information centre mechanisms (Brown 1986, Waltz 1987), and just one such study is available for communal roosts (Rabenold 1987). Nonetheless, several elegant and more recent studies now provide observations that are consistent with the idea that communal roosts act as information centres. Marzluff et al. (1996) experimentally made some common ravens *Corvus corax* knowledgeable by releasing them at newly created food sites, and kept others naïve by holding them captive for 2–30 days. After visiting a communal roost, dominant knowledgeable birds led roost mates to the food sources on several occasions. In another study on common ravens, Wright et al. (2003) observed that common ravens that discovered carcasses engaged in pre-roost display flights and initiated early morning departures. Successive observations suggest that information on the location of carcasses was obtained by naïve birds that roosted close to the knowledgeable birds. Communal roosts of hooded crows *Corvus corone cornix* also appear to act as information centres. Sonerud et al. (2001) created an unpredictable and ephemeral food distribution and radio-tracked 34 hooded crows. They report that naïve birds that roosted with knowledgeable birds (i.e. birds that had discovered food sites on their own) were more likely to find food sites than when no knowledgeable roost mates were present. Buckley (1997) reports that black vultures *Coragyps atratus* benefit from communal roosting because they were able to locate food by following knowledgeable conspecifics to carcasses.

GENERALISING THE INFORMATION CENTRE HYPOTHESIS

The previous section shows that empirical evidence for the ICH is available only for birds that face very patchy and temporary food conditions (i.e. carrion feeding corvids and vultures). Communal roosts as information centres might also be advantageous under less extreme foraging conditions. Moreover, the empirical evidence mostly focuses on advertent information transfer communicated through signals. For example, the aerial displays at common ravens roosts. Even if they represent advertisements of foraging opportunity, such signals might advertise individual quality and thus increase the chance of finding a high-quality mate (Marzluff et al. 1996, Wright et al. 2003). In agreement with Evans (1982) and Waltz (1982, 1987) information does not need to be actively transferred. Indeed, inadvertent information (Valone 1989, Danchin et al. 2004) might be a more general and likely source of information at communal roosts. Inadvertent information can be available as food carried in the beak or claws, distended crops, foraging frequency, and body condition (see Mock et al. 1988).

By its very nature, inadvertent information cannot be withheld by the providers and therefore its use at communal roosts can be an ESS (Lachmann et al. 2000). As long as the pay-off for roosting communally outweighs that of solitarily roosting, individuals will return to communal roosts and thereby reveal inadvertent information to the potential benefit of roost mates. Moreover, under various conditions birds may even be forced to

Table 5.1 The power of observational components to falsifying the generalised Information Centre Hypothesis based on the taxonomy proposed by Mock et al. (1988).

ICH component	Critique	References	Essential
1 Site fidelity	Innate differences in foraging abilities, such as the efficiency in locating food sites, could exist between individuals (e.g., adults and juveniles). Unsuccessful individuals can then follow skilled individuals to increase foraging success, and thus site fidelity is not essential for an information centre mechanism.	Weatherhead (1983), Rabenold (1987)	no
2 Differential success	–		yes
3 Detection	Ward & Zahavi (1973) argue that successful foragers actively advertise their foraging success to aid detection by unsuccessful foragers. Even though differential behaviour between successful and unsuccessful individuals can facilitate information sharing, behavioural differences are not a necessary condition. An unsuccessful individual could randomly select a roost mate to follow and thus increase foraging success. In addition to active information transfer, unsuccessful roost mates could use inadvertent information.	Waltz (1982), Waltz (1987) and Mock et al. (1988)	no
4 Synchronous departure	Synchronous departures can be mitigated by weather, tidal regime, precise language, limited compass directions, variable predation risks, etc. Therefore, it is not an essential component for support nor falsification of the ICH.	Bayer (1982), Mock et al. (1988) and Richner & Heeb (1995)	no
5 Following	As opposed to strict following to the exact foraging site, the general direction that a (successful) roost mate takes can provide information on foraging success. Following should be seen more generally as adjusted behaviour.	Ward & Zahavi (1973)	maybe
6 Toleration	Competitively better foragers could use competitively inferior roost mates to locate food sites. At the foraging site the latter information suppliers could be displaced by the competitively more able followers. Such inferior individuals could keep returning to communal roosts, because roosting solitarily is more costly. Toleration at food sites is thus not an essential component of the ICH.	Weatherhead (1983)	no
7 Pay-off	The (long-term) pay-off of information use does not need to be positive for communal roosts to function as information centres. This depends entirely on the total costs and benefits of communal roosting versus those of solitary roosting. For instance, the information pay-off could be negative, but as long as the pay-off of roosting solitarily is more negative than that of communal roosting, communal roosts can exist and could possibly function as information centres.	Danchin et al. (2008)	no

return to communal roosts. In coastal areas, for example, shorebirds are forced to retreat to areas not submerged during high tide (van de Kam et al. 2004, van Gils et al. 2006b). Because information at the communal roost is inadvertent, cheating by withholding information is not possible and punishing cheaters becomes irrelevant which increases the likelihood of reciprocal behaviour. The principle holds even for large communal roosts with variable membership. Given these conditions, we suggest that the ICH should be generalised such that: (1) besides advertent information, communal roosts are information centres for inadvertent information, and (2) communal roosts can be seen as information centres on foraging opportunities, but also on other types of information (e.g., on predators, timing of migration, potential mates, etc.).

Mock et al. (1988) suggested a seven-link chain of events to falsify the ICH. Here, we argue this falsification chain should be abandoned, because most of the components do not suffice for falsifying the general concept that communal roosts act as information centres (Table 5.1). Instead, we propose two essential components which can be used for its falsification: (1) differential success and (2) adjusted behaviour. First, differential success establishes that successful individuals have information and unsuccessful individuals are in need of this information. Second, information becomes meaningful if it results in behavioural change. Therefore, unsuccessful individuals should adjust their behaviour according to the gathered information. Information transfer can be falsified if it can be shown that members of a communal roost do not comply with one of these two components. Note that the long-term pay-off (component 7, Table 5.1) for individuals in communal roosts does not need to be positive for communal roosting to be an ESS as long as the pay-off for roosting solitarily is lower.

Inadvertent social information on foraging

There are many ways in which inadvertent social information may be used by individuals to improve their foraging success. For instance, unsuccessful individuals could benefit from inadvertent social information by following the fattest roost mates to their foraging sites. Besides fatness, any other cue can be used when it is a reliable indicator of foraging success (below, we provide examples based on arrival time at the roost). Unsuccessful foragers can even follow randomly selected roost mates to increase foraging success, assuming that they have an estimate of their relative foraging success. When unsuccessful foragers decide to search for a new food patch, they face the problem that such a patch could be located in every direction from the roost. By following a random roost mate they are more likely to arrive at a food patch, while saving the costs of searching for one. Moreover, previously unsuccessful birds will have lower site-faithfulness than successful birds and departure directions would be skewed towards more rewarding food sites (Waltz 1982, 1987). Therefore, the chances of finding a better food site are larger than finding one that is worse in case an unsuccessful individual (i.e. a birds with lower than median foraging success) follows a random roost mate to its foraging area. An individual needs only a measure of median foraging success in the surrounding environment and of one's own success, which might be as simple as body condition or intake rate at the previ-

ously visited patch. It has been shown that animals are able to assess foraging success and adjust foraging decisions accordingly (Valone 1989, Galef and Giraldeau 2001, Coolen et al. 2003, van Gils et al. 2003b, Valone 2006).

Other kinds of social information

In communal roosts other kinds of social information than foraging information can be available. Here we give some examples of social information that could be available to the benefit of roost members.

As proposed for breeding colonies, communal roosts might function as "hidden leks" where extra-pair copulations could occur (Wagner 1993), and public information on the quality of mates and the distribution of potential mates can be obtained. This could increase the likelihood of choosing the best mate and thereby increase fitness (White 2004). For instance, there is evidence that communal roosting reduces costs of mating and territory acquisition in red-billed choughs *Pyrrhocorax pyrrhocorax* (Blanco and Tella 1999). Indeed, finding a mate at a communal roost might be easier than away from it (Møller 1985). After the breeding season, the proportion of juveniles within a communal roost might also provide public information on breeding habitat quality surrounding the roost. Black-legged kittiwakes *Rissa tridactyla* were able to estimate breeding habitat quality by observing breeding success of neighbours within a breeding colony (Boulinier et al. 2008). Members of a communal roost could also assess potential opponent quality (Valone and Templeton 2002). Contests might occur over food, territories, nest sites or mates. These contests can be time- and energy-consuming, and might entail a risk of injury (Krebs and Davies 1993). An individual can benefit by obtaining information on fighting ability of possible opponents by observing contests between other individuals (i.e., eaves-dropping, Johnstone 2001).

Roosting communally can also provide information on the timing of migration to allow synchronised departures (Helm et al. 2006). Carefully timed migrations may decrease predation risk (Leyrer et al. 2009), and synchronous departures – enabling flight in structured flocks (Piersma et al. 1990) – may help reduce flight costs (Cutts and Speakman 1994, Weimerskirch et al. 2001). The advantages of synchronized departure and group flight during migration can also apply to commuting between roosts and food sites.

Information on the timing of moult might also provide fitness benefits through its synchronization. Mallards *Anas platyrhynchos* are stimulated to moult by the presence of moulting flock mates (Leafloor et al. 1996). Moulting reduces flight ability and thus increases the risk of predation. By moulting synchronously, an individual reduces the risk of predation compared to when moulting alone.

Selective learning may help to increase reproductive success for communally roosting birds when different types of song are available (Catchpole 1986, Hasselquist et al. 1996). Songs of male brown-headed cowbirds *Molothrus ater* differ between populations, and females are more responsive to male song from their own population than from other populations. Similarly, female cowbirds developed a preference for song types typical of their cage mates (see Galef and Laland 2005).

Information on potential predators might be available in communal roosts as well. This can be especially beneficial when a novel predator enters the habitat. Through fright behaviour from roost mates, such a predator can be identified without direct exposure (Griffin 2004).

Supply and demand of information

Within a communal roost certain members might have information that others are in need of. The supply and demand of information can vary with individual, species, time and location. During winter, information on food may be more important than information on potential mates. At the beginning of a breeding season priorities would change. Moreover, the higher the benefit of information – or the higher the costs of acquiring this information through trial and error – the higher the demand will be, and the higher the adaptive significance of communal roosts as information centres. Given the diversity in temporally fluctuating information, its sum can provide year-round information benefits in communal roosts. The available information, either advertent or inadvertent, can be used without direct benefit to the information provider. Alternatively, both the supplier and the receiver(s) of information can directly benefit from the exchange of information. In such a case communal roosts could be seen as information markets (Noë and Hammerstein 1994, Seppänen et al. 2007). For instance, successful foragers might negotiate foraging information with unsuccessful individuals for premium roosting positions (e.g., safety from predators sensu Weatherhead 1983). Or successful common ravens could negotiate a share of discovered carcasses with unsuccessful individuals in return for displacement of competitors at the carcass through group size, i.e. gang foraging (Wright et al. 2003, Dall and Wright 2009).

CONCEPTUAL MODEL: USING ROOST ARRIVAL TIMING AS INFORMATION ON INTAKE RATE, FORAGER STATE, AND PATCH AND DIET CHOICE

In this section we present a framework to guide future empirical studies on information use at communal roosts by illustrating how roost arrival timing may convey information on *where*, *with whom* and *on what* to forage. We demonstrate the framework by presenting a conceptual model based on what we already know about red knots *Calidris canutus* (hereafter called knots) in the Dutch Wadden Sea, but it is applicable to a wide range of communally roosting species.

Where to forage?

The time necessary for individuals to achieve their daily required energy intake depends on their average instantaneous energy intake rate. If we assume that knots are time-minimisers (sensu Schoener 1971, for which there is evidence as shown in van Gils et al. 2003a, van Gils et al. 2005b), aiming to collect no more than the amount of energy which they are going to spend, and that the rate of expenditure does not vary between individuals, then their daily foraging time is a good predictor of their energy intake rate.
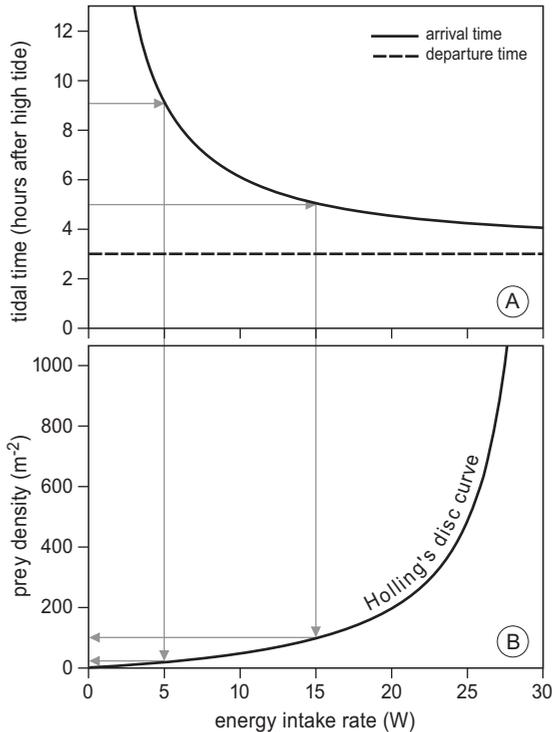
Figure 5.1 (A) Conceptual model showing how arrival time of red knot at communal roosts can give an estimate of past intake rate. Arrival time (h after high tide) can be predicted, given that knots are time-minimisers, leave the roost simultaneously 3 h after high tide, have equal energy requirements of 3.5 W (Piersma et al. 2003), and that 1.93 tidal cycles fit in 24 h. (B) Via Holling's disc equation (Holling 1959), linking intake rates to prey densities, average prey densities encountered by roost mates can be estimated using arrival times at communal roosts (see two such estimates shown as arrows going from panel A to B). The following parameters were used for Holling's functional response model: energy contents equals 300 J per prey, handling time equals 10 s, and searching efficiency equals 0.001 m^2 s^{-1}.

Furthermore assuming that all birds leave the roost together after high tide such that variation in foraging time is reflected in roost arrival times, roost arrival time becomes a direct function of intake rate (Fig. 5.1A). Individuals with high intake rates will return to the roost earlier, because they need less time to suffice their requirement. If a forager faces no other constraints on its intake rate than the rate of finding and the rate of handling food, then Holling's type II functional response (Holling 1959) couples the "expected intake rate" to an "expected prey density" (Fig. 5.1B), and thus roost arrival times can be indicators of prey density (Fig. 5.1B). A prediction resulting from this model would be that at the subsequent low tide period, unsuccessful foragers would follow individuals that had arrived at the roost early.

With whom to forage?

Currently, it is increasingly acknowledged that Holling's type II functional response model ignores an important constraint that many foragers may face. Most species are constrained by their digestive processing capacity before prey encounter rate or handling time become limiting (Jeschke et al. 2002). The red knot typically forages on molluscs buried in the sediment of intertidal mudflats (Zwarts and Blomert 1992, Piersma et al. 1993a). Once discovered, molluscs are swallowed whole and crushed in their muscular gizzards (Piersma et al. 1993b). The size of the gizzard constraints digestive processing rates (van Gils et al. 2003a, van Gils et al. 2005b), therefore, intake rate is not only a function of prey density, but also of gizzard size (Fig. 5.2A). At intermediate and high prey densities, the variation in intake rate is determined by gizzard size and not by prey density. In such cases, arrival time can give an estimate on gizzard size (Fig. 5.2B). A prediction that follows is that arrival times will be negatively dependent on gizzard sizes. Data from a radio-tracking study confirmed the presence of this negative relationship (Fig. 5.2C, based on van Gils et al. 2005b). Additionally, the birds leave the high-tide roost together, which is consistent with the assumption that knots minimise their time at the return to the roost rather than at their departure (Fig. 5.2C). For species that face a digestive constraint, information on individual state (i.e. digestive capacity) could be useful, for instance, because foraging with individuals in similar state could provide synchronization of behaviour. Given similar prey types and densities, individuals with large gizzards have higher intake rates than individuals with small gizzards. Therefore, individuals with larger gizzards satisfy their required intake quicker than individuals with smaller gizzards, and will return to the communal roost earlier (Fig. 5.2B). The consequence for an individual with a relatively small gizzard joining birds with large gizzards would be to remain on the food site alone with possible increased predation risk, or return to the roost unsatisfied. Of course, the question remains, if gizzard size and not food density determines intake rate, why different individuals go to different patches. All patches would anyhow yield the same intake rate, as determined by a bird's gizzard size. In case of the knot, the answer to this question lies in the variation in food *quality*.

On what food type to forage?

Prey can differ in quality (i.e. the amount of energy per gram indigestible shell mass) and patches of low and high quality can be found (Fig. 5.3A). Whenever high-quality prey is collected at a slower rate than low-quality prey (e.g., because densities of high quality prey are lower), this leads to gizzard-size-dependent optimal patch choice (van Gils et al. 2005b). Knots with small gizzards would maximize their energy intake rate in patches containing slowly collected high-quality prey, while birds with large gizzards would maximize their energy intake rate in patches containing rapidly collected low-quality prey (Fig. 5.3B). In such cases, gizzard-size-dependent patch choice would be expected. Indeed, published data reveal that knots with small gizzards forage on patches with high-quality prey, and knots with large gizzards forage on patches with low-quality prey (Fig. 5.3C, based on van Gils et al. 2005b). Arrival timing is a function of gizzard size, and could thus
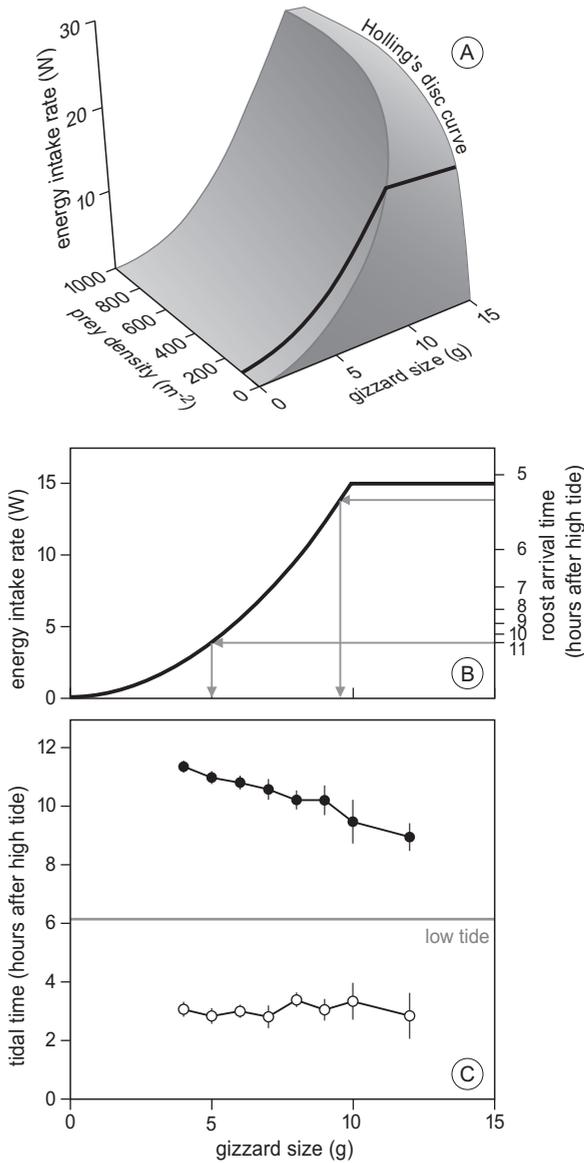
Figure 5.2 (A) The functional response taking digestive processing capacity into account. At low prey densities red knot intake rate is constrained by Holling's disc equation, but at higher prey densities by digestive processing capacity (i.e. gizzard size). The black line indicates an example intake rate as a function of gizzard mass (g) at a fixed prey density of 100 m^{-2}. (B) The black line in (A) is plotted here in a 2-D perspective. Given that individuals are digestively constrained, gizzard size determines intake rate and can be estimated from arrival times (arrows). The digestive constraint is empirically derived as: 0.05·q·gizzard mass^2 (van Gils et al. 2003a), where q denotes prey quality which equals prey energy content divided by shell content, the latter here set at 100 mg per prey, yielding a value for q of 3 J/mg. (C) Field data of red knot departure and arrival timing from their high-tide roost at Richel. Independent of gizzard mass, knots leave Richel about 3 h after high tide (open circles ± SE). Arrival times back at the roost are as predicted qualitatively (panel B): a declining function of gizzard mass (filled circles ± SE). Quantitatively there is still some mismatch between the predictions and field data, where birds with large gizzards are arriving somewhat later than predicted. Possibly this is because large gizzards incur higher metabolic costs which are not included in the simplified predictions. Data taken from van Gils et al. (2005b).
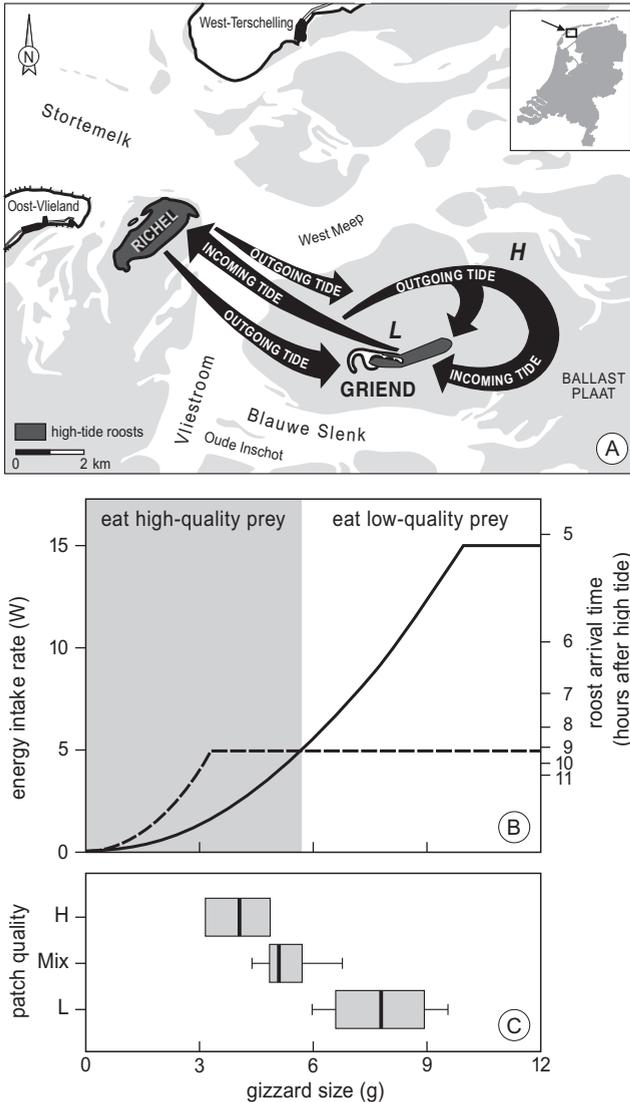
Figure 5.3 (A) Summary of typical red knot foraging itineraries in the western Dutch Wadden Sea, The Netherlands. The figure is taken from Piersma et al. (1993a). The arrows show red knot tidal movements during incoming and outgoing tides. The intertidal area is indicated by shading and bordered by the mean low-water mark at spring low tide. The two high-tide roosts on Richel and Griend are indicated in black. A patch containing low quality food (L) and a patch containing high quality food (H) are indicated based on van Gils et al. (2005b). (B) Arrival times as indicators of food quality. The predicted intake rates are given for the high quality food patch (dashed line; prey quality 9 J mg^{-1}) and the low quality food patch (solid line; prey quality of 3 J mg^{-1}). When high-quality prey occurs in lower densities than low-quality prey, rate-maximizing patch choice depends on gizzard size. In this case, knots with small gizzards (grey surface on the left) should feed at patches with low densities of high-quality prey, while knots with large gizzards (white surface on the right) should feed at patches containing high densities of low-quality prey. Arrival times can give an estimate of gizzard size and with that an estimate of food quality. (C) Field data of patch choice as a function of gizzard mass. The high quality prey patch (H) was only visited by knots with small gizzards, and the low quality prey patch (L) was only visited by knots with large gizzards. Knots with intermediate gizzards visited both patch L and H (mix). Data were taken from van Gils et al. (2005b).

give an estimate of the quality of food that roost mates encountered (Fig. 5.3B, also between years it has been found that food quality determines daily foraging times, van Gils et al. 2007). Given that individuals aim to maximise intake rate, naïve or unsuccessful knots could find the optimal prey type that matches their digestive capacity by following informed roost mates in similar state (i.e. gizzard size) during outgoing tide. A prediction would then be that knots with small gizzards follow individuals arriving at the roost late, but that individuals with large gizzards would follow individuals arriving early.

DISCUSSION

Many studies have attempted to show support for the ICH by investigating roost-departure timing (see Mock et al. 1988, Richner and Heeb 1995). The results, however, remain equivocal because firm predictions were lacking (Mock et al. 1988, Danchin and Richner 2001). Our conceptual model is oversimplified, but meets our purpose of providing a framework to study information use at communal roosts and allow for testable predictions. Some initial predictions would be that (1) a relationship exists between arrival timing and intake rate, forager state, and food quality (and prey density to a certain extent), (2) after observing arrival timing, naïve individuals will follow those individuals to food patches that have similarly sized gizzards. Our study system with knots seems well suited to test such predictions.

Our proposed framework could be applicable to other communally roosting species constrained by available foraging time. This includes corvids gathering food during daytime (Wright et al. 2003), owls hunting at night (Wijnandts 1984), grebes showing crepuscular foraging (Piersma et al. 1988), and shorebirds foraging during low tide (van de Kam et al. 2004, van Gils et al. 2005b). Roost-arrival timing is relatively easy to quantify in the field, but a major challenge will be to identify newly arrived individuals with respect to their prior knowledge and to understand how arrival timing conveys information on intake rate, prey density, forager state, food quality, etc. Another challenge will be to fit these and other kinds of information (e.g., predation risk, moult, mates and travel companions) into this framework. For instance, foraging decisions are usually state-dependent with respect to predation risk (Brown 1988, Olsson et al. 2002), and therefore arrival time at the roost and patch choice may convey information on predation risk. Under a food-safety trade-off without digestive constraints, time-minimization leads to late arrival times under a relatively low risk of predation, and early arrival times under a relatively high risk of predation. Furthermore, such information on predation risk is detectable if animals are able to judge each other's relative vulnerability to predation, e.g., body shape and condition (mass), and moult and plumage states, presumably reflecting the risk (or danger in the terminology of Lank and Ydenberg 2003) that they accepted during their foraging trips. A possible prediction would thus be that individuals in similar state follow each other. These individuals could then benefit in two main ways. First, knowledgeable individuals in a similar state (i.e. body weight) are more likely to have found the optimal food patch given the food-safety trade-off. Thus, naïve birds following knowledgeable

birds can reduce the costs of finding such an optimal patch. Second, in case of a predator attack individuals with a relatively large risk of predation (e.g., relatively large body mass, advanced state of primary moult) could avoid being the least manoeuvrable in a group with increased mortality risk by foraging with individuals in similar state.

In this contribution, we have argued to move beyond the original ICH to study the ecological implications of information transfer on food, predators, travel companions and mates in communal roosts. We hope our conceptual model stimulates further development of theory (including, e.g., stochasticity of the environment), generating more quantitatively testable predictions.