Social information, social feeding, and competition in group-living goats (*Capra hircus*)

Adrian M. Shrader,[a] Graham I.H. Kerley,[a] Burt P. Kotler,[b] and Joel S. Brown[c]
[a]Centre for African Conservation Ecology, Department of Zoology, PO Box 77000, Nelson Mandela Metropolitan University, Port Elizabeth 6031, South Africa, [b]Mitrani Department of Desert Ecology, Blaustein Institute of Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion 84990, Israel, and [c]Department of Biological Sciences, University of Illinois, Chicago, IL 60607, USA

There are both benefits (e.g., social information) and costs (e.g., intraspecific competition) for individuals foraging in groups. To ascertain how group-foraging goats (*Capra hircus*) deal with these trade-offs, we asked 1) do goats use social information to make foraging decisions and 2) how do they adjust their intake rate in light of having attracted by other group members? To establish whether goats use social information, we recorded their initial choice of different quality food patches when they were ignorant of patch quality and when they could observe others foraging. After determining that goats use social information, we recorded intake rates while they fed alone and in the presence of potential competitors. Intake rate increased as the number of competitors increased. Interestingly, lone goats achieved an intake rate that was higher than when one competitor was present but similar to when two or more competitors were present. Faster intake rates may allow herbivores to ingest a larger portion of the available food before competing group members arrive at the patch. This however, does not explain the high intake rates achieved when the goats were alone. We provide 2 potential explanations: 1) faster intake rates are a response to greater risk incurred by lone individuals, the loss of social information, and the fear of being left behind by the group and 2) when foraging alone, intake rate is no longer a trade-off between reducing competition and acquiring social information. Thus, individuals are able to feed close to their maximum rate. *Key words:* fear, group foraging, harvest rates, intraspecific competition, social information. *[Behav Ecol 18:103–107 (2007)]*

For herbivores, the biggest challenge of foraging may not be in finding food but in finding food of high quality within a mosaic of abundant low-quality food. Lone individuals must rely on experience and direct sampling (termed personal information; Valone 1991). On the other hand, individuals foraging in a group may have the added benefit of monitoring the foraging of others. Group members thus acquire "social information" (Clark and Mangel 1986; Valone 1993; Smith et al. 1999; Giraldeau et al. 2002; Dall et al. 2005). By using social information, individuals may be able to better locate patches (i.e., local enhancement; Poysa 1992; Giraldeau 1997) and assess patch quality (i.e., use public information; Valone 1989; Valone and Templeton 2002) than if they were on their own.

Other benefits of group living may include increased safety through higher levels of vigilance (the "many-eyes" hypothesis; Pulliam 1973), the dilution effect (Pulliam and Caraco 1984), or by keeping group members between predators and oneself (i.e., selfish herd effect; Hamilton 1971). In addition, by joining and moving with conspecifics, naive individuals may reduce costs associated with dispersal by gaining from the experience of residents (Shrader and Owen-Smith 2002).

There are, however, costs associated with foraging in a group. Valone (1993) suggested that individuals might abandon good patches prematurely as they try to remain part of a group. Smith et al. (1999) recorded this in captive red crossbills (*Loxia curvirostra*) when successfully foraging individuals abandoned patches in response to the departure of unsuccessful group members. A model designed by Beecham and Farnsworth (1998) indicated that strong group bonds may restrict an individual's patch choice and ultimately may result in short-term reductions in intake. In trying to maintain group bonds, sheep may feed in less-preferred patches (Dumont and Boissy 2000) and on less-preferred foods (Scott et al.1995).

Group feeding may also add a cost of intraspecific competition (Skogland 1985). The aggregation of conspecifics within rich food patches may result in interference and a more rapid depletion of the patch. This may be especially prevalent if herbivores monitor other group members and respond by moving into already occupied patches. Fritz and de Garine-Wichatitsky (1996) found that as group size increased, impalas (*Aepyceros melampus*) obtained less bites from individual bushes (i.e., patches). Molvar and Bowyer (1994) found that moose (*Alces alces*) spent less time foraging as group size increased due to increased aggressive interactions. The presence of others in a resource patch encourages each forager to maximize its instantaneous harvest rate even if this compromises long-term harvest rates (e.g., Mitchell 1990). An individual's preoccupation with current intake rates keeps it from losing out to competitors on the best feeding opportunities. Given the group size, impala responded to competitors by selecting from the subset of bushes offering the highest group size–specific gain (Fritz and de Garine-Wichatitsky 1996).

With these 2 costs in mind, we ask, how do social herbivores adjust their intake rate in light of the cost of having attracted by other group members (i.e., potential competitors)? In addition, does group size (i.e., number of competitors) affect the degree to which individuals adjust intake rate? To address these questions, we first determine whether a domestic herbivore, the goat (*Capra hircus*), uses social information to make foraging decisions. We then increase the number of potential competitors to see how individual intake rates change. If goats monitor other group members, we would expect them to utilize patches shown by conspecifics to be of high quality. In

response to increased competition, we predict that individuals currently feeding in a good patch should increase their instantaneous intake rate. This would allow them to obtain a larger amount of food available in the patch before other group members can harvest these opportunities.

METHODS

Experiments ran from 19 to 24 September 2005 in the semi-desert Riemvasmaak, Northern Cape Province, South Africa. During the day, goats in the Riemvasmaak range free without herders, and foraging trips may be up to 20 km round-trip from the kraal (i.e., corral) where they spend the night. During these feeding excursions, goats may encounter predators such as caracal (*Felis caracal*) and black-backed jackal (*Canis mesomelas*). In the late afternoon, goats return to their kraals where they stay overnight.

We tested the goats' use of 1) personal information, 2) social information, and 3) the influence of perceived competition on intake rate. Goats took part in the experiments in the morning prior to their daily foraging trip. We conducted the experiments using a 162-m^2 kraal fenced with wire mesh and divided into two 81-m^2 sections (Figure 1). Prior to the experiments, we habituated 49 goats to feed from plastic trays (600 × 400 × 180 mm). To limit intake rates, we attached a grid of 3 × 3 strands of 2.5 mm galvanized wire over the top of each tray and added 4l of dried corncobs as an inedible substrate. Food consisted of commercially produced sheep pellets (Veekos, BPK, Upington, South Africa).

We designed the experimental setup to best test the different hypotheses. The design mimics the visual contact that goats keep with each other while foraging in the field and the experiences that can occur when up to 6 goats feed from the same tree or shrub.
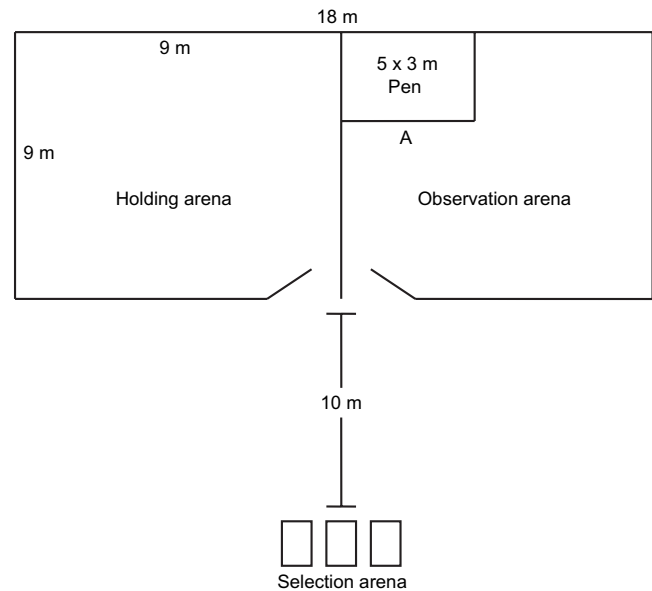
Personal information experiment

To test for the use of personal information, we used 3 trays of varying quality. Trays were spaced 1 m apart and placed outside (hereafter referred to as the selection arena) 10 m in front of the entrance to one of the kraal sections (hereafter referred to as the observation arena; Figure 1). From left to right, these trays had initial food abundances of 520 g, 130 g, and no food. Prior to the experiment, we moved all 49 goats into the other half of the kraal (hereafter referred to as the holding arena) and then surrounded the holding arena with black plastic sheeting. This prevented the goats from seeing into either the observation or selection arenas. We then moved a single goat into the observation arena where it could see the 3 trays. On releasing this goat into the selection arena, we recorded the first tray it selected. We repeated this procedure for each goat. As the goats did not have any prior knowledge of how much food was in each tray, we expected their first tray choice to be random with respect to initial food abundance.

Social information experiment

The following day, we tested the use of social information by removing the black plastic sheeting from the holding arena. Trays were set up in the selection arena as they were in the personal information experiment. However, for this experiment, we changed the distribution of food among the 3 trays. We put 130 g of food in left tray, no food in the center tray, and 520 g in the right tray. This prevented the goats from using prior knowledge about the location of food.

To start with, we released 2 goats into the selection arena and allowed them to feed from the 3 trays. The remaining 47

Figure 1
Kraal (18 × 9 m) where the experiments were conducted. We divided the kraal into two 9 × 9–m sections (i.e., holding and observational arenas). For the personal and social information experiments, we placed 3 trays 10 m in front of the kraal (i.e., selection arena). For the competition experiment, we built a 5 × 3–m pen in the observational arena and placed a tray (indicated by "A") against the fence.

goats left in both the observation and holding arenas were able to watch these goats eat. After 15 min, we removed the 2 goats and restocked the trays. The remaining 47 goats were then released from the observation and holding arenas individually. We once again recorded the first tray that each goat selected, but this time allowed it to eat for 3 min. The goats were able to monitor where the other individuals fed. In between testing each goat, we restocked each of the trays. If the goats in the observation and holding arenas watched goats in the selection arena and gained useful information, we would expect that a majority of them would select the tray with the most food when given their chance in the selection arena.

Competition

For the competition experiment, we constructed a 5 × 3–m pen within the observation arena (Figure 1). To simulate the effects of competition, we placed a tray within the larger section of the observation arena and against the fence of the small pen. We put 130 g of food in the tray and allowed each goat to feed individually for 3 min. On the first day, the small pen was empty. To provide an increasing perception of competition pressure from other goats without actually affecting food availability, we increased the number of goats in the small pen from 1 to 2 and then to 4 individuals over the next 3 days. The wire mesh of the fence allowed these goats to see and get their mouths through the fence. Nevertheless, it prevented them from harvesting any of the food from the tray. After the 3 min, we collected and weighed the food remaining in the tray and calculated intake rates (g/min).

Data analysis

We used a chi-square test to determine whether the goats selected the trays randomly during both the personal and social

information experiments. We also performed a chi-square test of independence to determine whether tray choice was dependent on the availability of information. For the competition experiment, we used repeated measures analysis of variance, coupled with Tukey honestly significant differenced (HSD) post hoc contrasts and polynomial contrasts, to analyze the variation in intake rate with the number of competing goats present. No significant effects of age, sex, or individual goat were found. We used linear regression to extrapolate intake rate when goats fed without competitors. Data were square-root transformed to achieve normality.

RESULTS

### Personal information and social information experiments

As expected, the goats distributed themselves equally among the 3 trays when they had no prior information from watching other goats eat ($\chi^2 = 5.39$; $P = 0.067$; $N = 46$). This distribution (no food = 18 goats, 130 g = 20 goats, 520 g = 8 goats) was almost unequal as goats tended to neglect the tray containing the most food. In contrast, when they were able to first watch others select and feed from trays, 30 out of the 44 goats selected the tray with the most food ($\chi^2 = 24.04$; $P < 0.0001$; $N = 44$). The remaining 14 goats distributed themselves equally between the other 2 trays. Overall, the choice of tray was dependent on the availability of social information (χ^2 test for independence; $\chi^2 = 23.8$; degree of freedom = 2; $P < 0.0001$; $N = 90$), indicating that goats used social information when selecting patches.

Competition

Number of competitors significantly affected intake rate (mean square [MS] = 634.33, $F_{3,111} = 21.06$, $P < 0.001$). Intake rate increased linearly with the number of potentially competing goats (MS = 686.59, $F_{1,37} = 17.58$, $P < 0.001$, first-degree polynomial contrast) ranging from 7 g/min for one competitor to 16 g/min for 4 competitors (Figure 2). However, a significant nonlinearity (MS = 957.95, $F_{1,37} = 39.94$, $P < 0.001$, second-degree polynomial contrast) showed that the intake rate for a goat by itself (13 g/min) was higher than in the presence of one potential competitor (MS = 1255.81, $F_{1,37} = 27.77$, $P < 0.001$, Tukey HSD post hoc contrast). This value did not differ from intake rates when in the presence of 2 (11 g/min) or 4 (16 g/min) potential competitors (MS = 58.21, $F_{1,37} = 0.32$, $P = 0.58$, Tukey HSD post hoc contrast). When we extrapolated back from one or more competitors to when goats were alone (i.e., no competitors), we underestimated actual intake rate by 9 g/min (slope = 3.06, intercept = 4.14, $F_{1,132} = 55.71$, $P < 0.0001$, $R^2 = 0.30$; Figure 2).

DISCUSSION

Group living confers various benefits and costs onto social foraging. By using social information, goats may be better able to locate high-quality food than if they were solitary. Yet, when feeding in groups, herbivores face increased competition and potentially restricted patch use (Skogland 1985; Beecham and Farnsworth 1998). We found that, similar to other group-feeding species (Galef and Giraldeau 2001; Valone and Templeton 2002; Coolen et al. 2005), goats benefit from the use of social information when making foraging decisions. Such foragers may typically need to choose between using personal information or social information, depending on which is more reliable (Kendal et al. 2004; van Bergen et al. 2004; Coolen et al. 2005; Webster and Hart 2006). Such complica-
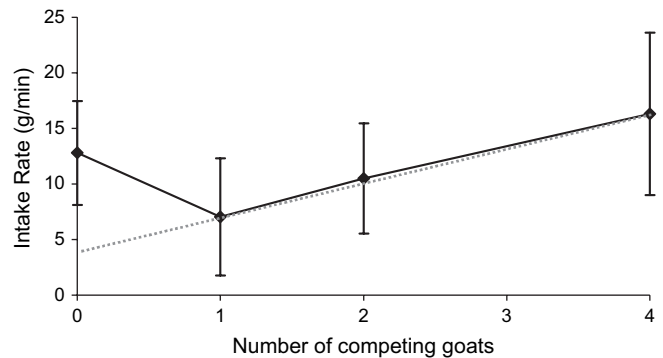
Figure 2
Changes in intake rate ($\bar{x} \pm$ standard deviation) in relation to the number of competing goats present. The dotted line indicates the expected intake rate, generated through linear regression (slope = 3.06, intercept = 4.14, $F_{1,132} = 55.71$, $P < 0.0001$, $R^2 = 0.30$) using the intake rates when one or more competing goats were present.

tions may make the interpretation of information use difficult. However, that was not a concern here because during our study, the goats had no prior personal experience or information from the patches and thus could utilize only social information to make their foraging decisions. As foragers monitor each other, individuals are likely to be aware that other group members will notice when they themselves find high-quality patches. To compensate for the presence of group members, we found that goats increased their intake rate as the number of these potential competitors increased from 1 to 4.

This, however, raises the question, why do the goats not maximize their intake rate across all social circumstances? We suggest 3 possibilities for when they are feeding within a group. First, by increasing feeding rate, individuals reduce the time they can spend observing other goats foraging and hence reduce the amount of social information they can obtain. The more goats there are, the more information is potentially lost. Second, if goats feed at a fast rate, they are more likely to attract other goats to the patch and decrease its quality. Third, by feeding quickly, they reduce both personal vigilance (more valuable than social vigilance; Fitzgibbon 1989) and the amount of social vigilance that they can benefit from as it may become more difficult to notice the distress of others while feeding so intently.

Distances between group members reflect a balance between protection from predators and competition for food (Beecham and Farnsworth 1998). Goats increased their intake rate in the presence of group members in a manner likely to reduce losses in food intake associated with competition. Faster intake rates would allow them to ingest a larger portion of the available food both before competing group members could arrive and later in their presence.

In contrast, the higher intakes achieved by lone goats cannot be explained by competition. To address this, we provide 2 potential explanations for the higher feeding rate of lone individuals.

The first explanation arises from a combination of social information and fear (Brown and Kotler 2004, forthcoming). Lone individuals lose out on the benefits of social information. When individuals can use social information (i.e., when they are part of a group), they can better direct their efforts toward rich patches (Poysa 1992; Giraldeau 1997), assess patch quality (Valone 1989; Valone and Templeton 2002), and thus forage more efficiently.

In addition, lone individuals left behind by the others are at greater risk. By living in groups, herbivores can reduce the possibility of being preyed on through the dilution effect

(Bertram 1978; Dehn 1990), increased vigilance (Pulliam 1973; Lima 1995), or through the selfish herd effect (Hamilton 1971). To obtain these benefits, individuals must remain in close proximity to other group members. If individuals remain feeding in a patch after the group moves away, their potential danger will increase because of the loss of proximity to others. Similarly, individuals on the edge of groups tend to have higher vigilance levels than do centrally placed individuals (Prins and Iason 1989; Bednekoff and Ritter 1994; Burger and Gochfield 1994; Hunter and Skinner 1998). Lingle (2001) found that in the presence of coyotes (*Canis latrans*), group cohesion in mule deer (*Odocoileus hemionus*) increased, with individuals moving closer together and forming more tightly bunched groups. In addition, coyotes typically attacked individuals that were in outlying positions (>10 m away from the group) or alone.

Possibly, when alone, goats obtained high intake rates because they feared being left behind by the group. Underwood (1982) suggested that for African grazers, isolated individuals, or those in small groups separated from the main herd likely look to rejoin the herd rapidly. This could be done by employing a higher quitting harvest rate for patch departure and by harvesting food more quickly while foraging within the patch. The high intake rate generated due to this fear suggests that, at least for goats, the short-term costs of fear are equal to competing with two or more group members.

Ultimately, herbivores make trade-offs between obtaining a high instantaneous intake rate and the level of personal vigilance they maintain (Underwood 1982; Fortin et al. 2004). This becomes evident as they try to maintain group bonds. As the group moves away, herbivores may prefer to take advantage of group benefits of social information and lower predation risk and thus immediately abandon the patch in which they are feeding. In contrast, they may instead sacrifice personal vigilance, and thus increase predation risk, to obtain a few extra bites and to shorten the time before they rejoin the herd. The level of predation risk will depend not only how far away the group is but also on the size of the group. Benefits will likely be a function of the richness of the patch.

Another example arises in the face of increasing competition. When herbivores find high-quality patches, they may lower their personal vigilance in order to increase intake rate, first to obtain more food before other competitors arrive and then to obtain a greater share while the patch is being jointly exploited. An interesting dilemma for herbivores is the degree to which group size affects this trade-off. In small groups, as more competitors move into a patch and increase their intake rates, the total amount of social vigilance may decrease. Depending on the availability of resources in the patch, eventually individuals will have to decide between ingesting food and maintaining some level of vigilance. This, however, is unlikely to apply to large herds where single food patches would not be able to provide enough resources for all individuals.

A second potential explanation is that intake rate is a trade-off between 1) intraspecific competition, 2) time spent acquiring social information, and 3) digestive constraints. When feeding alone, there is no social information to obtain, and foragers can match harvest rate with the appropriate digestive constraints that most affect harvest rate (Afik and Karasov 1995; McWilliams et al. 1999; McWhorter and del Rio 2000). Thus, solitary individuals would be able to feed at a faster rate that would maximize digestive efficiency.

We have demonstrated that goats can access social information and use it to locate high-quality patches. Furthermore, we found that goats altered their feeding dynamics in the presence of group members. More group members represent more competition as well as more social information. Foragers respond to more competitors by increasing intake rate in the current patch and perhaps by sacrificing personal vigilance

levels in the process. Nonetheless, the benefits of group living are such that lone foragers increase their harvest rates while foraging in a patch, perhaps in an effort to rejoin the group as quickly as possible or because they do not need to attend to social information. The benefits of group living, especially the value of social information, are strong drivers of these behavior patterns.

REFERENCES

Afik D, Karasov WH. 1995. The trade-offs between digestion rate and efficiency in warblers and their ecological implications. Ecology. 76:2247–2257.

Bednekoff PA, Ritter R. 1994. Vigilance in Nxai Pan springbok *Antidorcas marsupialis*. Behaviour. 129:1–11.

Beecham JA, Farnsworth KD. 1998. Animal foraging from an individual perspective: an object orientated model. Ecol Model. 113:141–156.

Bertram BCR. 1978. Living in groups: predator and prey. In: Krebs JR, Davies NB, editors. Behavioural ecology: an evolutionary approach. 1st ed. Oxford: Blackwell. p. 122–147.

Brown JS, Kotler BP. 2004. Hazardous duty pay and the foraging cost of predation. Ecol Lett. 7:999–1014.

Brown JS, Kotler BP. Forthcoming. Foraging and the ecology of fear. In: Stephens D, Ydenberg R, Brown JS, editors. Foraging. Chicago (IL): University of Chicago Press.

Burger J, Gochfield M. 1994. Vigilance in African mammals: differences among mothers, other females and males. Behaviour. 131:154–169.

Clark CW, Mangel M. 1986. The evolutionary advantages of group foraging. Theor Popul Biol. 30:45–75.

Coolen I, Ward AJW, Hart PJB, Laland KN. 2005. Foraging nine-spined sticklebacks prefer to rely on public information over simpler social cues. Behav Ecol. 865–870.

Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW. 2005. Information and its use by animals in evolutionary ecology. Trends ecol evol. 20:187–193.

Dehn MM. 1990. Vigilance for predators: detection and dilution effects. Behav Ecol Sociobiol. 26:337–342.

Dumont B, Boissy A. 2000. Grazing behaviour of sheep in a situation of conflict between feeding and social motivations. Behav Process. 49:131–138.

Fitzgibbon CD. 1989. A cost to individuals with reduced vigilance in groups of Thompson's gazelles hunted by cheetahs. Anim Behav. 37:508–510.

Fortin D, Boyce MS, Merrill EH, Fryxell JM. 2004. Foraging costs of vigilance in large mammalian herbivores. Oikos. 107:172–180.

Fritz H, de Garine-Wichatitsky M. 1996. Foraging in a social antelope: effects of group size on foraging choices and resource perception in impala. J Anim Ecol. 65:736–742.

Galef BG, Giraldeau L. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim Behav. 61:3–15.

Giraldeau L. 1997. The ecology of information use. In: Krebs JR, Davies NB, editors. Behavioural ecology. London: Blackwell. p. 42–68.

Giraldeau L, Valone TJ, Templeton JJ. 2002. Potential disadvantages of using socially acquired information. Philos Trans R Soc Lond B. 357:1559–1566.

Hamilton WD. 1971. Geometry for the selfish herd. J Theor Biol. 31:295–311.

Hunter LTB, Skinner JD. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. Behaviour. 135:195–211.

Kendal RL, Coolen I, Laland KN. 2004. The role of conformity in foraging when personal and social information conflict. Behav Ecol. 15:269–277.

Lima SL. 1995. Back to basics on anti-predatory vigilance: the group-size effect. Anim Behav. 58:537–543.

Lingle S. 2001. Anti-predator strategies and grouping patterns in white-tailed deer and mule deer. Ethology. 107:295–314.

McWhorter TJ, del Rio CM. 2000. Does gut function limit humming-bird food intake? Physiol Biochem Zool. 73:313–324.

McWilliams SR, Caviedes-Vidal E, Karasov WH. 1999. Digestive adjustments in cedar waxwings to high feeding rate. J Exp Zool. 283: 394–407.

Mitchell WA. 1990. An optimal control theory of diet selection—the effects of resource depletion and exploitative competition. Oikos. 58:16–24.

Molvar EM, Bowyer RT. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. J Mamm. 75:621–630.

Poysa H. 1992. Group foraging in patchy environments: the importance of coarse-level local enhancement. Ornis Scand. 23:159–166.

Prins HHT, Iason G. 1989. Dangerous lions and nonchalant buffalo. Behaviour. 108:262–296.

Pulliam HR. 1973. On the advantage of flocking. J Theor Biol. 38: 419–422.

Pulliam HR, Caraco T. 1984. Living in groups: is there an optimal group size? In: Krebs JR, Davies NB, editors. Behavioural ecology. Oxford: Blackwell Scientific. p. 122–147.

Scott CB, Provenza FD, Banner RE. 1995. Dietary habits and social interactions affect choice of feeding location by sheep. Appl Anim Behav Sci. 45:225–237.

Shrader AM, Owen-Smith N. 2002. The role of companionship in the dispersal of white rhinoceros. Behav Ecol Sociobiol. 52:255–261.

Skogland T. 1985. The effect of density-dependent resource limitation on the demography of wild reindeer. J Anim Ecol. 54:359–374.

Smith JW, Benkman CW, Coffey K. 1999. The use and misuse of public information by foraging red crossbills. Behav Ecol. 10:54–62.

Underwood R. 1982. Vigilance behaviour in grazing African ungulates. Behaviour. 79:81–107.

Valone TJ. 1989. Group foraging, public information, and patch estimation. Oikos. 56:357–363.

Valone TJ. 1991. Bayesian and prescient assessment: foraging with pre-harvest information. Anim Behav. 41:569–577.

Valone TJ. 1993. Patch information and estimation: a cost of group foraging. Oikos. 68:258–266.

Valone TJ, Templeton JJ. 2002. Public information for the assessment of quality: a widespread social phenomenon. Philos Trans R Soc Lond B. 357:1549–1557.

van Bergen Y, Coolen I, Laland KN. 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. Proc R Soc Lond B Biol Sci. 271:957–962.

Webster MM, Hart PJB. 2006. Subhabitat selection by foraging three-spine stickleback (*Gasterosteus aculeatus*): previous experience and social conformity. Behav Ecol Sociobiol. 60:77–86.