Original Article

When should I be aggressive? A state-dependent foraging game between competitors

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INTRODUCTION

Competition has long been viewed as one of the most important driving forces that shape population dynamics and community structure (Gause 1934; Brown and Lieberman 1973; Gurevitch et al. 1992). In an ecological sense, competition means density-dependent negative effects of interactive organisms on each other's fitness (Connell 1983). Such negative effects can be caused by either depleting or directly preventing others from accessing shared resources, namely, exploitation competition and interference competition, respectively. Compared to exploitation competition, interference competition involves more forms and mechanisms, such as allelopathy, kleptoparasitism, depression of prey availability and disturbance in food searching (Goss-Custard 1980). Although largely ignored in most traditional theories on interspecific competition (Amarasekare 2002), interference competition has received increasing attention in recent decades (e.g., Frye 1983; Carothers and Jaksic 1984; Ruxton et al. 1992; Ziv et al. 1993; Adler and Mosquera 2000; Stillman et al. 2002; Vahl et al. 2005) and it is suggested that competition involving different mechanisms may cause different effects on population regulation and community organization (Hart 1987).

Interference competition often results in loss of foraging time or reduced intake rate and has long been included in the framework of foraging theory. An optimal forager should balance between foraging and other fitness-related behaviors such as mating, interference, and predation avoidance (Brown 1988). Ecological factors such as food distribution pattern, visibility of food and food handling time have proved important in affecting foragers' trade-offs between foraging and aggressive interference (e.g., Cresswell et al. 2001; Stillman et al. 2002; Vahl et al. 2005; Vahl et al. 2007; Gyimesi et al. 2010). However, foragers' individual states are likely equally important because a forager's assessment of the costs and benefits associated with its behavior is largely state dependent (e.g.,

energetic state: Berger-Tal et al. 2010; life stage: Herde and Eccard 2013; prior experience: Berger-Tal et al. 2014; breeding state: Eccard et al. 2011). Previous studies suggest that a hungrier forager should allocate more time to foraging and be more willing to take risks while foraging (e.g., Brown and Kotler 2004; Berger-Tal et al. 2010; Embar et al. 2014a) because of the higher marginal value of energy (Kotler et al. 2004; Berger-Tal and Kotler 2010). Similarly, given that aggressive behavior inevitably costs time and energy and often involves a potential risk of injury (e.g., Drews 1996; Briffa and Sneddon 2007), we should expect a hungry forager to be more tolerant of risk associated with aggressive interference than well-fed foragers when competing for shared food, all else being equal.

However, all else may not be equal. Because interference competition inevitably involves 2 or more individuals, the outcomes of competition for 1 competitor are also affected by other competitors' behavior. In this sense, an optimal forager should also take the states of other competitors into consideration, which results in a state-dependent foraging game between competitors. Various models of foraging games have been developed (e.g., Gilliam and Fraser 1987; Hugie and Dill 1994; Brown et al. 1999; Bouskila 2001; Brown et al. 2001) and certain state-dependent foraging games have been experimentally verified in recent years (e.g., Berger-Tal et al. 2010; Embar et al. 2014a, 2014b). However, these studies generally focus on predator–prey systems, whereas the state-dependent foraging game between intra-guild competitors has not been empirically verified.

Consider a system including 2 foragers competing on depletable food patches in an environment where predation risk can be ignored, with one forager (dominant competitor) individually superior to the other (subordinate competitor) in aggressive encounters. Food items are nutritious and storable, mixed into inedible substrate so that foragers would face a diminishing return. For convenience, we assume that the dominant competitor's risk of injury during contests can be ignored. We also assume that a contest happens only when the subordinate competitor attempts to forage and an attack is always initiated by the dominant competitor.

For the dominant competitor, aggressive behavior and foraging are mutually exclusive and spending more time on one means less on the other. The dominant competitor can choose to be more aggressive to monopolize the common resources but at the cost of higher metabolic cost and lower harvest rate (possibly a result of decreased foraging time and lower encounter rate due to interference). It, therefore, faces a challenge to balance between foraging and being aggressive. A well-fed dominant competitor should be more willing to invest on aggressive interference for resource protection rather than foraging because the marginal value of immediate energy intake is low. For the subordinate competitor, foraging chance is often associated with risk of aggression from the dominant competitor. For it, interference means not only higher metabolic cost and lower harvest rate, but also considerable risk of injury similar to predation risk. However, the subordinate competitor needs to tolerate such cost to some extent in order to acquire essential food for maintenance. The challenge now is to determine how tolerant of aggressive behavior it should be. According to Clark's "asset-protection principle" (Clark 1994), a forager in lower energetic state should be more willing to withstand risk associated with foraging. Meanwhile, the marginal value of food is perceived to be higher for a hungry forager, which also suggests that a subordinate competitor in lower energetic state should be more tolerant of aggressive behavior than a well-fed one should be.

Based on these analyses, we can further predict that in such a system 1) interference would be most aggressive (i.e., with the longest total duration or highest frequency of confrontation) when the dominant competitor is well-fed and the subordinate competitor is hungry, 2) the subordinate competitor will harvest most food items and forage most efficiently (i.e., with the highest average harvest rate or the lowest GUD) when both foragers are hungry, and (3) the dominant competitor will harvest most food items and forage most efficiently when it is hungry and the subordinate competitor is well-fed. Moreover, according to Brown's giving-up density (GUD) framework (Brown 1988), an optimal forager should stop foraging in a patch with diminishing returns when its instantaneous harvest rate no longer exceeds the sum of costs associated with foraging in that patch. The amount of food that a forager leaves in a patch (GUD) can be used to measure its perceived cost of foraging in that patch. Higher risk of injury during aggressive encounters, higher energetic consumption associated with competition and/or lower marginal value of energy would result in higher perceived cost of foraging. Under this scenario, we should expect that 4) both foragers possess higher GUDs when they are well-fed and 5) the subordinate competitor should possess higher GUDs when the dominant one is well-fed. Finally, it has been well-documented that aggressive behavior should increase as resource quality increases (Powers 1987; Gabor and Jaeger 1995; Berger-Tal et al. 2015), we then predict that 6) when foraging together, both competitors should possess higher GUDs in rich patches than in poor patches.

In this paper, we seek evidence of such an intra-guild foraging game in a desert rodent system. This system involves 2 species that coexist in several East Asian deserts: midday gerbil (*M. meridianus*) and 3-toed jerboa (*D. sagitta*). Gerbils are well-known for their agonistic behavior (Berger-Tal et al. 2015). Previous experience also tells us that *M. meridianus* can easily dominate *D. sagitta* in aggressive encounters (Shuai et al. 2016a). Both species are nocturnal, solitary, and mainly granivorous. In our study, gerbils and jerboas were grouped into pairs and each pair was allowed to forage in an indoor arena and compete for artificial food patches. We manipulated the energetic state of both species and explored whether and how energetic state affected the foraging and contesting behavior.

METHODS

The *M. meridianus* and *D. sagitta* individuals used in this study were all captured in August 2015 in the Gobi Desert in Gaotai County, Gansu Province, China. Before the experiment started, all the individuals had been maintained in our laboratory for at least 20 days. When not participating in the experiment, the animals were kept individually in separate plastic boxes (40 × 35 × 30 cm for gerbils and 55 × 40 × 35 cm for jerboas) with a sandy substrate and provided with *ad libitum* food (sunflower seeds, millet seeds, and fresh flowers of *Hedysarum scoparium*) and water. We selected 8 male gerbils and 8 male jerboas (gerbils: 42–51 g; jerboas: 52–58 g) and randomly grouped them into 8 pairs. Grouping was fixed and the animals were nonbreeding throughout the study.

We performed our experiment in September 2015 in 4 (5 × 5 m) indoor arenas. Before each trial, each arena was provided with 2 aluminum trays (30 × 30 × 5 cm), which served as artificial food patches for rodents. The trays were placed near the center of the arena and the distance between the trays was 40 cm. Each tray contained 4 L of sifted fine sand within which unhusked sunflower seeds were thoroughly mixed. In each arena, we placed 16 seeds in the west-side tray to generate a rich patch and 4 seeds in the east-side tray to generate a poor patch. To better mix the seeds in poor patches, each tray was divided into 2 × 2 subareas (15 × 15 × 5 cm

for each) and a seed was randomly buried in 1 subarea, but with a distance of 15–25 cm between seeds. We used 2 trays instead of a single tray to prevent dominant competitors from monopolizing resource too easily (e.g., monopolizing all the resource simply by staying in a patch), without showing detectable aggressive behavior. Sunflower seeds instead of millet seeds (which have been widely used in studies on the foraging behavior of desert rodents) were used as food items for 2 reasons: first, they are similar in size to a favorite food (seeds of *H. scoparium*) of these 2 species in the field; second, their relatively large size enabled us to measure the exact quantity of food items consumed by each individual during the experiment. However, seeds with such a large size might be too easy to find and, therefore, fail to generate diminishing returns, a necessary assumption for our study. Fortunately, our results showed that this was not the case: when foraging alone, both species possessed GUDs from 1 to 3 items/tray (Table 1).

Our experiment included 2 periods: the training session and the formal experiment. Each period consisted of 4 experimental nights and each individual was used in 1 trial per night. The aim of the training session was to allow all the animals to become familiar with the trays and the arenas. In this session, each individual participated in a trial on 4 consecutive nights. During each night (from 1900 h to 2350 h) in this session, each individual was given 1 h to forage alone in an arena. The sequence of individuals in each night was randomly determined. We also altered the arena where each individual foraged from day to day so that after the training session, each individual had experience foraging in all 4 arenas. Each individual was deprived of food (but with access to water) 20 h prior to each trial. By the end of this session, all the animals were ready to forage in trays and we then considered the training session to have been successful. The behavior of each animal in its fourth trial of the training session was used for analysis to provide baseline information on its intrinsic foraging traits.

The formal experiment started 2 days after the training session. Manipulation of individuals' energetic states was required during this session. We conducted our experiment every 3 nights to better manipulate individuals and to ensure independence among nights. We produced a "hungry" animal by depriving it of food 20 h (but with access to water) before the following trial, and we produced a "well-fed" animal by allowing it to forage freely in its cage with access to *ad libitum* food and water until the following trial started. The energetic states of both individuals in a pair were fully crossed, and this methodology resulted in 4 combinations of treatments: both hungry (hereafter, H–H); both well-fed (hereafter, F–F); hungry gerbil + well-fed jerboa (hereafter, H–F); and well-fed gerbil + hungry jerboa (hereafter, F–H). For each group, the sequence of the 4 combinations of treatments was randomly selected.

Between 1930 h and 2230 h on each experimental night, 2 trials were conducted in each arena (altogether 8 trials per night) and

each pair of animals participated in just 1 trial. The sequence of pairs each night was randomly determined, and each pair was assigned to all 4 arenas during the 4 nights. At the beginning of each trial, we introduced a pair of rodents simultaneously into an arena. At the end of each trial, we immediately placed the animals back in their own cages with access to *ad libitum* food and water. We then sifted and counted the seeds remaining in each tray. Sand, food, and trays were renewed before each trial started. Between trials, we carefully removed debris in arenas and washed the ground with diluted bleach. Our study adhered to the ABS/ASAB guidelines for the treatment of animals in behavioral research and teaching (2012). Ethics approval was given by Animal Ethics Committees at Institute of Zoology, Chinese Academy of Sciences (approval number: IOZ14001).

We used infrared video cameras to monitor and record animal behavior throughout the experiment. For each individual in each trial, we collected the following information by slowly replaying video clips: 1) duration of each food tray visit and total patch residence time (defined as the sum of duration of tray visits for each individual during each trial, to the nearest 0.1 s), 2) foraging time for each food tray visit (defined as the time spent on digging and food handling by each individual during each food tray visit, to the nearest 0.1 s) and total foraging time, 3) number of seeds harvested, 4) average harvest rate (defined as the number of seeds harvested divided by the total patch residence time, in unit s^{-1}; however, gerbils occasionally carried food items away from the patches to consume them; thus, we added the time they spent on food handling out of the patches to the denominator to enable the interspecific comparison), 5) duration (to the nearest 0.1 s) of each event of confrontation and total duration of confrontation, 6) outcome (which individual finally withdrew) of each event of confrontation, 7) frequency of confrontation, and 8) GUD in each tray. GUD was defined as the number of seeds remained uneaten in a tray when an individual finally ceased foraging in that tray. However, the GUD results should be considered exploratory rather than definitive, because the duration of each trial was rather short (each trial was subject to a time limit of 1 h) and we were not sure whether the animals really gave up foraging when a trial ended. The relatively few food items originally provided in each patch (especially the poor patch) might also make the GUD results less reliable.

For the training session, we conducted paired-samples *t*-tests to assess the effects of species on the number of seeds harvested, GUDs and average harvest rate. Mann–Whitney *U* tests were used for dependent variables with abnormal distributions (total residence time and total foraging time).

For each species in the formal experiment, Anovas were used to test for the effects of gerbil state, jerboa state, identity of group, and all the second-ordered interactions on the following behavioral variables: total time spent in trays, total time spent foraging, number of seeds harvested, average harvest rate, frequency of confrontation, and GUDs in both patches. We conducted multiple Anovas instead of Manova because most of the behavioral indicators are conceptually independent. However, such a procedure would cause potential inflation of Type I error so that those marginally significant effects should be treated more cautiously. A Friedman test was conducted to explore whether the total duration of confrontation (similar for both species) differed among treatments.

Values of variables throughout the text are reported as the mean ± standard error. All the statistical analyses were conducted with SPSS 19 (SPSS Inc., Chicago, IL).

Table 1

Summary of foraging behavior (mean value ±1 SE) of *M. meridianus* and *D. sagitta* in training session (*n* = 8)

	M. meridianus	*D. sagitta*
Total time spent in trays (s)	694.65 ± 67.05	1116.54 ± 49.48**
Time spent foraging (s)	642.50 ± 62.68	1005.88 ± 54.23**
Number of seeds harvested (item)	16.50 ± 0.57	15.00 ± 0.78
Average harvest rate (item/s)	0.0193 ± 0.001	0.013 ± 0.003**
GUD in rich patches (item)	2.13 ± 0.72	3.00 ± 0.57
GUD in poor patches (item)	1.38 ± 0.46	2.00 ± 0.27

**P < 0.01 (interspecific comparison).

RESULTS

We mainly report significant results and effects here. Complete Anova tables can be found in Supplementary Material. Table 1 summarizes main results of the training session.

Patch residence time and foraging time

When foraging alone, gerbils exhibited a significantly shorter total patch residence time (Mann–Whitney U test: $\mathcal{Z} = -3.36$, $P = 0.001$) and total foraging time (Mann–Whitney U test: $\mathcal{Z} = -2.94$, $P = 0.003$) than jerboas did (Table 1).

When foraging together, both species spent significantly more time in food patches when hungry than when well-fed (gerbil: $F_{1,7} = 92.20$, $P < 0.001$; jerboa: $F_{1,7} = 37.66$, $P < 0.001$; Figure 1). Hungry rodents also exhibited a longer total foraging time than well-fed ones (gerbil: $F_{1,7} = 71.27$, $P < 0.001$; jerboa: $F_{1,7} = 15.15$, $P < 0.01$; Figure 1). Gerbil state and jerboa state interacted to affect jerboas' foraging time ($F_{1,7} = 5.71$, $P = 0.05$). Hungry jerboas exhibited a longer total foraging time when gerbils were hungry (paired-samples t-test: $t = 3.14$, degree of freedom (df) $= 7$, $P = 0.016$), whereas well-fed jerboas did not respond significantly to gerbil state (Figure 1). Gerbils did not respond significantly to jerboas' energetic state in terms of total residence time ($F_{1,7} = 1.84$, $P = 0.22$) or total foraging time ($F_{1,7} = 0.49$, $P = 0.51$).

Food harvest, average harvest rate, and food handling

When foraging alone, the 2 species showed no significant difference in the number of seeds harvested per trial (paired-samples t-test: $t = 1.40$, df $= 7$, $P = 0.20$; Table 1). However, gerbils exhibited a significantly higher average harvest rate (paired-samples t-test: $t = 6.37$, df $= 17$, $P < 0.001$; Table 1).

When foraging together, both species harvested more seeds (gerbils: $F_{1,7} = 121.78$, $P < 0.001$; jerboas: $F_{1,7} = 42.07$, $P < 0.001$; Figure 2) and exhibited higher average harvest rates (gerbils: $F_{1,7} = 19.48$, $P = 0.003$; jerboas: $F_{1,7} = 8.78$, $P = 0.021$; Figure 2) when hungry than when full. Gerbil state and jerboa state interacted to affect jerboas' food harvest on a marginally significant level ($F_{1,7} = 4.31$, $P = 0.08$). Hungry jerboas harvested significantly more seeds when gerbils were hungry (paired-samples t-test: $t = 3.00$, df $= 7$, $P = 0.02$; Figure 2). Averagely, jerboas harvested most seeds in H–H treatment (5.00 ± 0.50 items), followed by F–H (2.75 ± 0.37 items), H–F (0.88 ± 0.30 items), and F–F (0.63 ± 0.38 items). However, the energetic state of gerbils did not significantly affect the jerboas' average harvest rate ($F_{1,7} = 2.32$, $P = 0.17$). Gerbils did not respond to the energetic state of jerboas in terms of the number of seeds harvested ($F_{1,7} = 0.39$, $P = 0.55$) or average harvest rates ($F_{1,7} = 1.53$, $P = 0.26$). On average, gerbils harvested more seeds per trial than jerboas when foraging together (gerbils: 8.81 ± 0.97 items; jerboas: 2.31 ± 0.37 items; paired samples t-test: $t = 6.66$, df $= 31$, $P < 0.001$).
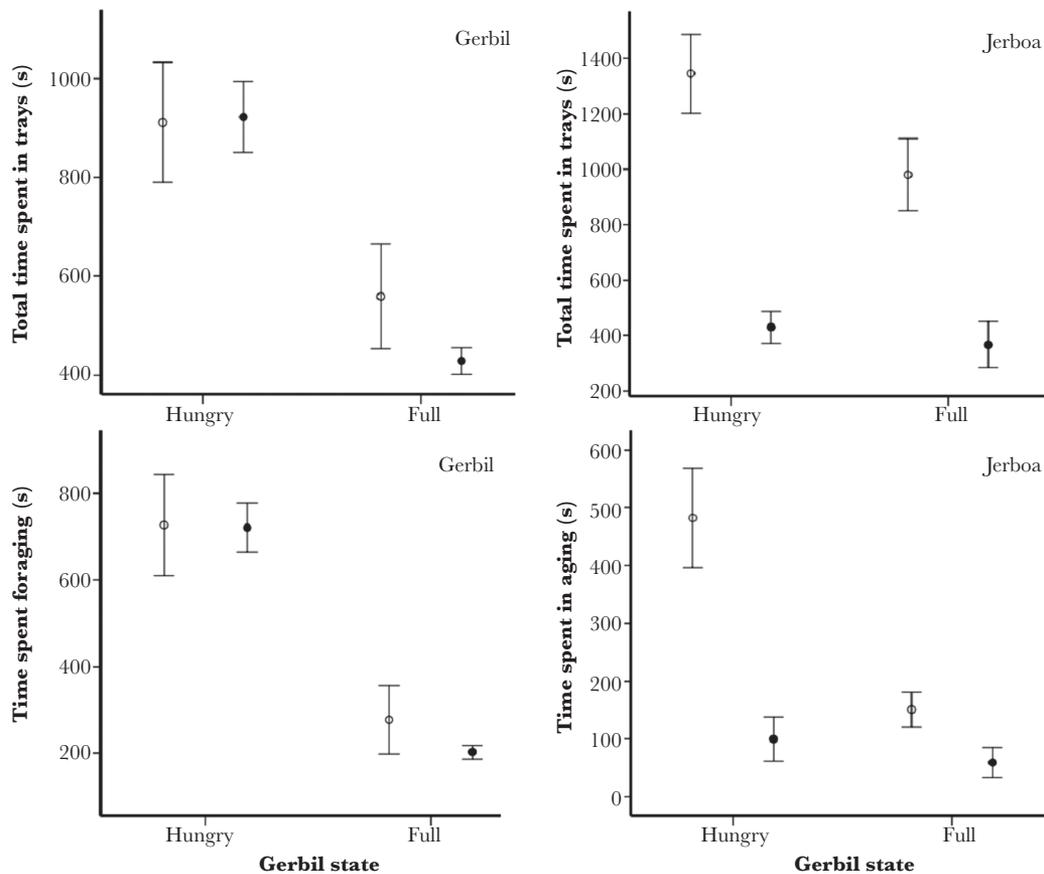
Figure 1
Interactions between the effects of gerbil state and jerboa state on the total time spent in trays (up) and time spent foraging (bottom). The horizontal axis indicates gerbil states. Solid and open circles represent full jerboas and hungry jerboas, respectively. Error bars represent ± 1 standard error (SE).
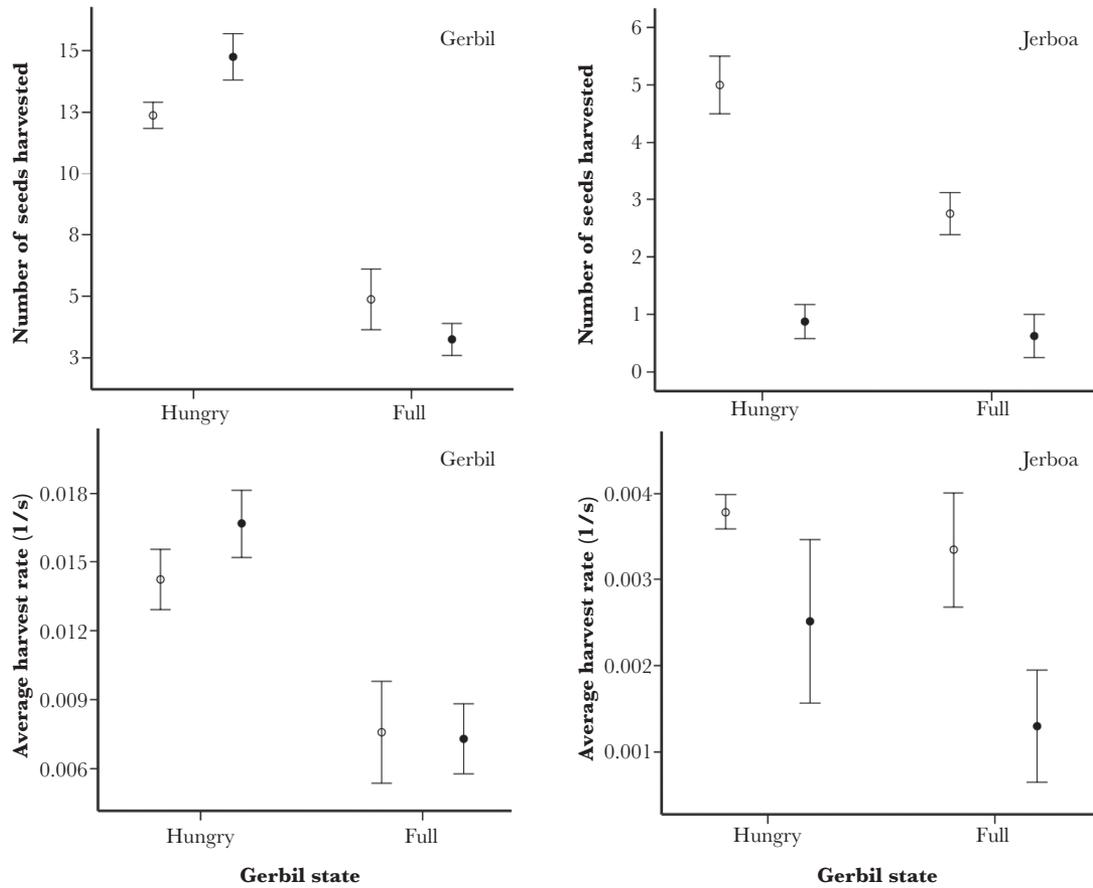
Figure 2
Interactions between the effects of gerbil state and jerboa state on the number of seeds harvested (up) and average harvest rate (bottom). The horizontal axis indicates gerbil states. Solid and open circles represent full jerboas and hungry jerboas, respectively. Error bars represent ±1 SE.

When foraging alone, gerbils carried away most of seeds they found (proportion of seeds carried away: 82.79 ± 5.61%) and consumed them elsewhere (usually near the base of a wall). However, they tended to consume most of the seeds they found (proportion of seeds carried away: 4.29 ± 2.52%, 0.00 ± 0.00%, 3.04 ± 2.16%, and 0.00 ± 0.00% for H–F, F–H, H–H, and F–F, respectively) immediately in the patches when foraging with jerboas. In contrast, jerboas always consumed seeds right away in the patches, regardless of the presence of gerbils.

Contesting behavior

We totally recorded 943 events of confrontation. Without exception, gerbils always acted as attackers and won all the direct confrontations against jerboas. In more than 95% of the cases, jerboas withdrew within 5 s once gerbils started to attack. The total duration of confrontation significantly differed among the 4 treatments (Friedman test: $\chi^2 = 21.75$, df = 3, $P < 0.001$; Figure 3). The mean values were highest under F–H (189.78 ± 44.50 s), followed by F–F (102.47 ± 23.96 s), H–H (58.87 ± 18.01 s), and H–F (37.08 ± 10.93 s). Gerbils attacked jerboas more frequently when they were well-fed ($F_{1,21} = 24.11$, $P < 0.001$) or when jerboas were hungry ($F_{1,21} = 14.05$, $P = 0.001$; Figure 3).

GUD

When foraging alone, gerbils did not exhibit significant difference in GUDs between patches (paired-samples t-test: $t = 0.70$, df = 7,

$P = 0.50$; Table 1), whereas jerboas possessed higher GUDs in rich patches on a marginally significant level (paired-samples t-test: $t = 2.37$, df = 7, $P = 0.05$; Table 1). We detected no significant interspecific difference in GUDs (rich patch: $t = -0.88$, df = 7, $P = 0.40$; poor patch: $t = -1.17$, df =7, $P = 0.28$; paired-samples t-test).

When foraging together, both species significantly increased GUDs in both patches when they were well-fed (gerbils in rich patches: $F_{1,7} = 63.99$, $P < 0.001$; jerboas in rich patches: $F_{1,7} = 17.14$, $P = 0.004$; gerbils in poor patches: $F_{1,7} = 57.81$, $P < 0.001$; jerboas in poor patches: $F_{1,7} = 24.52$, $P = 0.002$; Figure 4). Jerboas also increased GUDs in rich patches when gerbils were well-fed ($F_{1,7} = 34.56$, $P = 0.001$; Figure 4), whereas gerbils did not change their GUDs in rich patches according to jerboa state ($F_{1,7} = 0.97$, $P = 0.36$). For both species, GUDs in rich patches were significantly higher than in poor patches (gerbil: $t = 6.14$, df = 31, $P < 0.001$; jerboas: $t = 8.33$, df = 31, $P < 0.001$; paired-samples t-test; Figure 4). Gerbils averagely possessed lower GUDs than jerboas in both trays (rich patches: $t = -2.83$, df = 31, $P = 0.008$; poor patch: $t = -2.24$, df = 31, $P = 0.032$; paired-samples t-test). However, as Figure 4 suggests, such a pattern was only significant when a hungry gerbil encountered a well-fed jerboa.

DISCUSSION

Our study empirically verifies that a state-dependent foraging game exists between intra-guild competitors. We simultaneously controlled the energetic states of both competitors and observed their
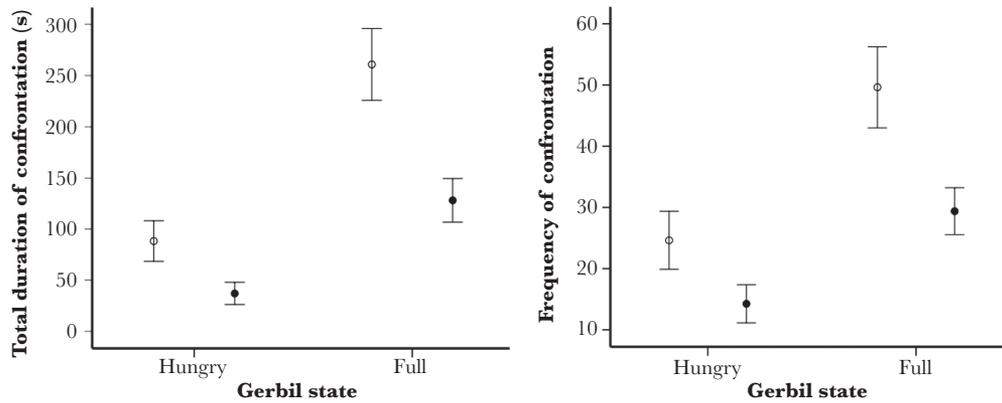
Figure 3

Interactions between the effects of gerbil state and jerboa state on the total duration of confrontation (up) and frequency of confrontation (bottom). The horizontal axis indicates gerbil states. Solid and open circles represent full jerboas and hungry jerboas, respectively. Error bars represent ±1 SE.
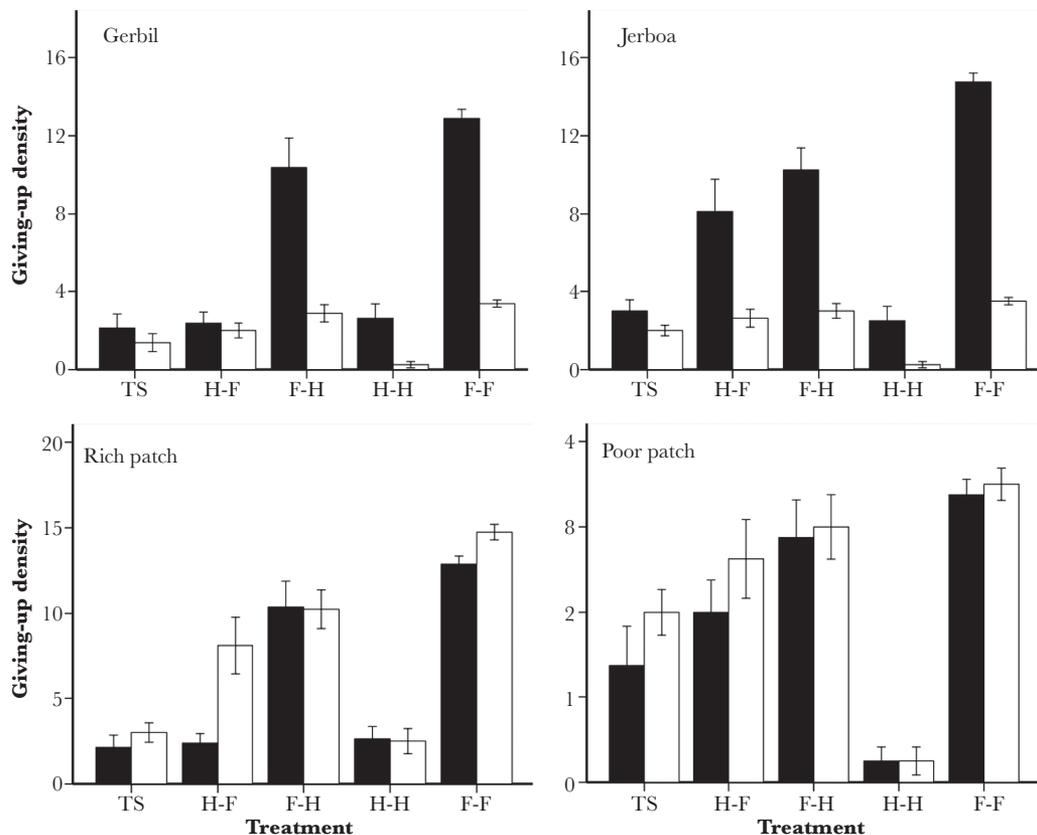
Figure 4

Up: comparisons between the GUDs in rich patches (black bars) and GUDs in poor patches (white bars) under different treatments; bottom: comparisons between the GUDs of gerbils (black bars) and jerboas (white bars) under different treatments. GUD here means the number of seeds remained in a tray when an individual ceases foraging in that tray. The horizontal axis represents 5 treatments: TS (training session), H–F (a hungry gerbil vs. a full jerboa), F–H (a full gerbil vs. a hungry jerboa), H–H (both individuals hungry), and F–F (both individuals full). Error bars represent ±1 SE.

behavioral responses. The results basically supported our predictions. In terms of foraging time, food harvest, and GUD, both species responded significantly to their own energetic state, and hungry jerboas also significantly responded to the state of gerbils. Gerbils were more aggressive when they were well fed or when jerboas were hungry. When foraging together, GUDs in rich patches were significantly higher than in poor patches, suggesting that interference was generally more intensive in rich patches. As our experimental design does not consider treatments of conspecific pairs, at this stage we cannot clearly attribute these behavioral patterns to

interspecific competition or just competition. Such a limitation will be addressed in our future study.

One of our previous studies suggests that there is an asymmetric competition between *M. meridianus* and *D. sagitta*, with the former being superior in interference competition and the latter superior in tolerating predation risk (Shuai et al. 2016a). The present study supports part of that finding. Gerbils in our study were clearly a superior competitor because they always initiated the attacks and generally won the contests without difficulty. In terms of food harvest and GUD, gerbils were also less affected by jerboas than jerboas that were

affected by gerbils. However, gerbils did change their foraging strategies when jerboas were present. In the training session, they preferred to carry food items away and consume them in a safe place (the "grab-and-go" strategy; St. Juliana 2005). This behavior is consistent with our previous field studies (Shuai and Song 2011; Shuai et al. 2016a) and a study on gerbils in the Negev Desert (Ovadia et al. 2001). In the formal experiment, however, they tended to consume food right away in food patches (the "eat-at-tray" strategy; St. Juliana 2005). Social foraging should be a reasonable explanation for this difference: when foraging with a competitor, it is wise for the dominant forager to remain longer in food patches in order to reduce the time that shared resources are left exposed to the competitor.

So when should a dominant competitor be aggressive in such an intra-guild interaction? It depends on the marginal value of aggression versus that of other behaviors, mostly foraging in the present study. Our results suggest that the most aggressive interference occurred when the dominant competitor was well fed and the subordinate one was hungry. For a superior competitor in a high energetic state, the marginal value of defending a resource of high future value is relatively higher than that of immediate food intake. Therefore, it may be a better choice to exclude other competitors than to leave a resource exposed to others. Meanwhile, note that jerboas' energetic states also played a role in shaping gerbils' decisions. Regardless of gerbil state, hungry jerboas tended to spend more time in trays, which unavoidably increased their chances in encountering gerbils. Accordingly, gerbils became more aggressive and spent more time to chase off these competitors. Overall, in our experimental setup, a hungry jerboa should be more willing to meet a hungry gerbil than a well-fed one, whereas a gerbil should be more aggressive when well fed or when encountering a hungry jerboa.

Morris (2009) first proposed the concept of apparent predation risk and stated that the risk associated with interference competition may act like a predation risk for subordinate competitors. Our study supports this idea: with gerbils present, jerboas spent less time on effective foraging and harvested less food, which is a typical response of several prey species under high predation risk (e.g., Kotler et al. 2004; Bakker et al. 2005). Our previous study suggests that in natural habitats, *D. sagitta* is generally able to cope with relatively high predation risk, whereas *M. meridianus* forages earlier and enjoys richer food patches (Shuai et al. 2016a). It seems that, in the system studied here, gerbils are mainly constrained by predation risk whereas jerboas are mainly constrained by apparent predation risk.

An often cited mechanism of coexistence is that a larger-sized forager should be better at interference, locomotion and/or antipredation, whereas a smaller competitor should possess advantages in foraging efficiency when resource density is low (e.g., Kotler and Brown 1988; Ziv et al. 1993; Basset 1995). Such a pattern is not supported by our studies. Although it is not clear why *M. meridianus* (the slightly smaller species) possesses advantages against *D. sagitta* in aggressive encounters, we think that some difference in locomotion and morphology may contribute to this pattern. For a jerboa, the bipedal locomotion and an excessively long tail may bring advantages in energy saving (Dawson and Taylor 1973; but see Thompson 1985), higher top speed (Djawdan and Garland 1988), or erratic escaping (Djawdan and Garland 1988), but they may also make it less nimble and easier to be attacked when staying in a small patch (Shuai, personal observation). In summary, it seems that gerbils and jerboas employ different solutions to the trade-off between interference and predation risk tolerance, which may be important in promoting their coexistence. In the Gobi Desert, the advantage in interference competition enables gerbils to occupy patches of high quality, whereas

the disadvantage in antipredation makes them unable to completely monopolize a patch, as suggested by their relatively high GUDs (Shuai et al. 2016a). Jerboas can thus benefit from their advantage in predation risk tolerance to forage in patches of low quality or when gerbils are absent (Shuai et al. 2016a). A somewhat similar case can be found in a North American woodland system featuring 2 squirrels, with fox squirrels (*Sciurus niger*, the larger species) better at antipredation and grey squirrels (*Sciurus caroliniensis*, the smaller species) better at competition (Lanham 1998; van der Merwe et al. 2005). As a result, habitat partitioning occurs between the 2 species, with *S. niger* more frequently observed in open forest or forest edges and *S. caroliniensis* more likely to be found in densely forested areas (Steele and Koprowski 2001). However, the underlying mechanism of such a trade-off between interference and predation risk tolerance and its potential role in promoting coexistence have not been well documented in previous studies and deserve more attention.

The state-dependent foraging game between competitors may seem similar to that between predators and prey (e.g., Berger-Tal et al. 2010). Both systems are asymmetric, with one player behaviorally dominant over the other. The subordinate players in both games are all responsive to the states of the dominant ones, whereas the dominant players may or may not respond to the states of the subordinate ones (e.g., Berger-Tal et al. 2010; Embar et al. 2014b). However, there is an important difference between these 2 types of foraging games. First, the apparent predation risk is caused by a dominant competitor, which often (although not always) consumes the common resource while excluding its opponent. In this scenario, the subordinate competitor loses not only foraging time but also the amount of resources left available. Take the present study as an example: jerboas averagely spent 1005.88 ± 54.2 s foraging and had access to 20 seeds per trial when gerbils were absent; however, these 2 numbers dropped to 198.03 ± 38.63 s and 11.19 ± 0.97 seeds when gerbils were present. Therefore, the negative effects of apparent predation risk on subordinate foragers may be more irreversible than in a predator–prey system (unless the prey is killed or greatly harmed by the predator). Second, the foragers in these 2 systems have different goals and, therefore, should adopt different strategies. In a predator–prey system, the goal of the predator is to maximize its possibility of killing the responsive prey within a time constraint. Generally, a hungry predator will be more aggressive than a well-fed one (Berger-Tal et al. 2010; Embar et al. 2014a). In an intra-guild foraging game, however, the competitors aim to harvest or protect the common resource as efficiently as possible, depending on their social status and energetic states. As our results suggest, unlike the predator, a well-fed dominant competitor should be more aggressive than a hungry one, because resource protection is now more important than foraging. Such differences between systems should lead to different evolutionarily stable strategies (ESS) with respect to time allocation or habitat use. Future studies comparing or linking these 2 different foraging games should be valuable.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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