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Are there self-imposed group foraging costs in the nutmeg mannikin (*Lonchura punctulata*)?

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ABSTRACT

Are there self-imposed group foraging costs in nutmeg mannikins (*Lonchura punctulata*)?

Shawn Gauvin

Animals that feed socially may benefit from the presence of others without necessarily improving their feeding rates. Feeding rates may actually decrease in the presence of others due to different forms of competition and interference (kleptoparasitism, aggression). Recent work with starlings (*Sturnus vulgaris*) shows that social foragers may also experience self-imposed costs to their feeding rates in order to remain in the presence of group members, despite a lack of physical interaction or overt aggression. I studied whether nutmeg mannikins (*Lonchura punctulata*) feeding from depletable patches alone or with a heterospecific or conspecific flock in a separate cage adjacent to the food patch experience such self-imposed feeding costs. The birds experienced self-imposed changes to their foraging behaviour which led to decreased feeding rates. Subjects fed more slowly in treatments with conspecifics despite travelling more quickly between patches. The decrease occurred because they spent more time idle near the flock instead of feeding from the patch or immediately travelling to the next one. This seems to be a cost related to the maintenance of group cohesion. The birds also reduced their scanning time and rate near conspecifics without experiencing a concomitant increase in feeding rate consistent with the group-size effect. This result may point to a form of interference usually

attributed to reduced quality of or access to the food resource caused by group members.

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INTRODUCTION

The behaviour of foraging animals is often influenced by the presence and population density of others. A large amount of research has been devoted to exploring the consequences of foraging in groups (Giraldeau & Caraco 2000). One common result of group foraging is the scanning-group-size effect in which individuals reduce the time spent scanning and increase their feeding rates as group sizes increase (Lima 1995, Roberts 1996, Schmaltz 2001). A cost of having competitors around is the potential for losing food through kleptoparasitism (Elgar 1989a, Triplet et al. 1999) which in turn modifies the food choices (Thompson & Barnard 1984) of potential hosts and possibly the composition of foraging assemblages (Ranta et al. 1995, Lindstroem & Ranta 1993). This occasionally leads to aggressive displacements or even escalated fighting (Sirot 2000). However, one of the most widespread consequences of the presence of competitors is interference (Stillman et al. 1996) - the reversible reduction in feeding rate that occurs as a result of the presence of competitors (Goss-Custard 1980). Interference should exclude reductions in feeding rates due to the depletion of resources by foraging competitors and should include only behavioural effects that reduce intake rates either because searching efficiency declines (Hake & Ekman 1988) or because handling time increases (Johnson et al. in press).

Field studies of interference are often hampered by uncontrolled associations between forager density and local food abundance (Ens & Goss-Custard 1984, Norris & Johnstone 1998). Controlled studies require experimental manipulation of competitor density and food abundance (Creswell 1997, 1998, Righetti et al. 2000).

However, even in controlled studies it is difficult to pinpoint the exact mechanism through which individuals interfere with each other. Cresswell (1997), for instance, documents the effect of interference in blackbirds (*Turdus merula*) foraging in the presence of others but could find no overt behavioural modification of the bird's foraging behaviour. Livoreil & Giraldeau (1997) studied patch exploitation by groups of nutmeg mannikins (*Lonchura punctulata*) in the laboratory and found that one member of each group of three birds they tested was strongly affected by the presence of companions. These so-called omega birds foraged much more slowly when in a group than alone. The authors interpret this lower feeding rate as interference caused by the presence of others but could not provide its mechanism or exclude food depletion as a cause.

Interference can be the consequence of reduced access to food but Vasquez & Kacelnik (2000) suggested it could also be the result of self-imposed changes to foraging behaviour that are required to remain social. Self-imposed effects refer to behavioural changes observed in an individual when in a situation where potential competitors are absent or cannot physically interact with the subject in a way that could cause the observed response. It is important to distinguish between these two responses because self-imposed social responses, if they exist, have been hidden effects and are difficult to identify as long as studies involve foragers sharing common food resources (Vasquez & Kacelnik 2000) as these seldom control for effects of patch depletion. To make this point, Vasquez & Kacelnik (2000) conducted an experiment using starlings (*Sturnus vulgaris*). The subjects' foraging consisted of alternating between two operant chambers with diminishing returns,

one of which was adjacent to a treatment cage that was either left empty or contained three starlings or three zebra finches (*Taeniopygia guttata*). The finch treatment served to test whether the presence of conspecifics had a different effect from that of a generalized social disturbance. The birds shuttled from one operant device to another through a 30 cm travel cage. Each feeder was programmed to require an increasing number of pecks to deliver food and feeders were reset whenever a bird started pecking at the alternative device. They found that starlings responded to the presence of other starlings by altering the time they spend away from the flock cage and argue that starlings forage more slowly in the presence of conspecifics because they forage much faster in the cage away from the conspecific companions. They conclude that their study demonstrated the existence of a truly self-imposed social foraging cost that raises questions concerning cost-benefit analyses of social foraging behaviour.

Their point is compelling but would have been stronger had the effects they report been observed at the social foraging patch rather than away from it. Moreover, the device they used made it difficult to distinguish between foraging and non-foraging time (time spent on the feeder and time spent away from the feeder when in the cage) due to the fact that the entire cage containing the feeder was referred to as the food patch. Though they recorded non-foraging time between entering the operant box and the first peck at the feeder and between the last peck at the feeder and departure from the operant box, any such absence of foraging activity would have gone undetected if expressed between successive foraging responses.

If subjects scanned less and pecked as quickly while at the feeder near companions as away from them but continually left and returned to the feeder to perch near the flock or spent more time looking in their direction there may be no increase in feeding rate as is the case away from conspecifics. This makes it impossible to determine if the subjects are interrupting their feeding to approach the flock or simply not pecking as quickly when a flock is present as when alone. Their apparatus and data recording make it impossible to determine exactly what combination of feeding time and non-foraging time is responsible for the observed effects. Moreover, the study lacks detailed behavioural records and presented the subjects with a rather simple environment in which the birds consumed food that required no handling besides swallowing and did not need to search for food items but simply responded to an operant device. This could have prevented detection of finer level responses that occur during food searching and that would normally be ascribed to interference.

I ask whether self-imposed social costs of group foraging noted for starlings (Vasquez & Kacelnik 2000) also occur in another social, ground-feeding bird, the nutmeg mannikin. I ask whether the presence of competitors affects the subject's scanning, allocation to foraging and non-foraging activity as well as the food searching behaviour in the patch. To do so I use an apparatus in which the food patches are spatially explicit allowing the observer to distinguish unambiguously between a bird's foraging and non-foraging activity. Moreover, the patches require searching for food which allows the observer to record the effect that competitors can have during food searching as well as record the time subjects spend scanning

and the direction of scans.

If nutmeg mannikins experience self-imposed costs of sociality I predict that they should feed more slowly when in the presence of conspecifics compared to heterospecifics or alone. The slower feeding rate could be the result of increased non-foraging time, increased vigilance, or reduced searching efficiency. I also predict that travel time toward the patch near conspecifics will be shorter than toward other patches. I expect heterospecifics to have no effect.

METHODS

Subjects

I used 11 wild-caught adult *L. punctulata* and three juvenile budgerigars (*Melopsittacus undulatus*) purchased from a commercial supplier. Birds were not sexed. All birds were individually identified with coloured leg bands, were kept in 59 x 32 x 46 cm (high) housing cages, and maintained on a 12:12 h light:dark cycle with *ad libitum* access to water and commercial seed mixtures outside of experiments. The eight subjects were kept in two housing cages of four birds. The six companion birds were housed by species in separate housing cages.

Apparatus

Two rows of three cages (like the housing ones) were placed adjacent to each other to create a u-shaped corridor in which two adjacent cages at one end were selected to be patch cages, each containing a food patch (Fig.1). To go from one patch to

another the birds had to travel through six cages, moving from one cage to the other through 11 x 9 cm (wide) openings. Adjacent to each patch cage I placed an additional housing cage to serve as a flock cage that, depending on treatment, would house companions or not. The flock cage remained inaccessible to the subjects. The outermost cage wall of the apparatus was covered by an opaque blind preventing subjects from seeing outside.

A food patch contained 20 white millet (*Panicum* spp) seeds hidden under a double layer of dried yellow peas placed in the bottom of a 10 cm petri dish. Subjects searched for the seeds among the peas and were expected to experience an increase in the time required to obtain each successive seed (ie: a decrease in feeding rate over time spent searching for seeds in the food patch) (Livoreil & Giraldeau 1997). I sat behind a tinted plexiglass window located adjacent to the patch cages allowing me to see the subjects but not the reverse (Fig. 1).

Training

The eight subjects were trained once per day, first in pairs and then individually, to feed alternatively from each food patch while flock cages remained empty. Thus, when trained individually, no other bird could be seen or heard from the test room. Subjects were food-deprived for 16-17 h (overnight + 4-5h) before training. Each bird flew from its holding cage to a separate transportation cage before entering the testing room. The subject then flew from this transportation cage directly into the apparatus. Thus subjects were never handled during the experiment.

At the start of each trial the apparatus contained two food patches. The subject exploited the first patch it came across and then travelled to the other. When a subject began feeding from the second patch, the first patch was withdrawn through a small opening in the blind using a small hook and a replenished patch was gently pushed back into place after which a flap of black opaque plastic covered the opening in the blind. Fully trained subjects flew back and forth between patches and were considered ready for testing when they exploited at least six patches consecutively without backtracking during interpatch travel. Training trials ended when a subject stopped foraging for five minutes.

Experimental Trials

The procedure for experimental trials was similar to that used in training. Subjects were tested individually and food-deprived for 16.5-17 h prior to tests. During trials, I noted behaviour verbally on an audio tape recorder and replays were used to enter observations into an event recorder (Noldus Observer).

The eight subjects experienced three different treatments: two companion treatments (one with conspecifics and one with budgies) in which one of the two flock cages contained companions, and a solitary treatment in which both flock cages were empty. The budgie companion treatment served the same purpose as the zebra finch treatment used by Vasquez & Kacelnik (2000) and hence acted as a control for the non-social effects that would have been generated by the presence of live animals, regardless of species. Every subject was submitted to six

experimental trials (companions on each side of the apparatus 3 times) of a given treatment and experienced a random sequence of the three treatments. I tested two subjects per day (one trial per day each) but continued the training of all other birds to keep them at maximum performance levels.

The following events were recorded during trials: the number and time of seed captures, time spent in each patch cage and in patches, the duration of travel in each direction and the duration of trials. During patch time I noted the frequency, duration, and orientation of scanning; when the head was held in an upright position (a projected line from the bird's eye through its nostril was parallel to or above the horizontal) (Coolen et al. 2001). Otherwise the bird's head was in a down position (line through the eye and nostril below the horizontal). When a bird scanned, I noted whether the scan was directed towards or away from the flock cage. Scanning was not measured when subjects were outside the food patch because birds could not feed outside the patches and therefore almost always had their head in an upright position.

A trial began when the subject entered the first feeding patch and ended when it left its 10^{th} patch or when it spent at least 5 min without visiting a patch. In the latter case this last 5 min was excluded from the analyses. These criteria were established during training when I determined that 1) a bird that stopped looking for patches for 5 consecutive min typically did not resume foraging for at least 30 min and could therefore be considered as satiated, and 2) no bird exploited more than 10 patches before it stopped foraging.

Cage time started when a subject entered a cage containing a food patch

and ended when the bird exited the cage. Patch time started whenever at least one of the following was true: the subject stood in, perched on the edge of, or held any part of its head above the patch. Patch time could be interrupted by a bird exiting the patch. However, if it returned to the patch without having left the patch cage, patch time resumed. Once a bird left the patch cage all patch times for that cage visit were summed and counted as one patch visit. I defined the feeding rate in the patch as the number of seeds obtained per patch time. Non-foraging time was calculated by removing patch time from cage time. A pecking time was calculated by excluding the time spent scanning from the patch time. Pecking rate, therefore, corresponds to the number of seeds taken per pecking time. Scanning was expressed as scan time- the proportion of patch time used for scanning, and as scan rate- scans per patch time.

Travel time was recorded in each direction and included only the time a bird spent in the travel cages (see Fig. 1). On the rare occasions where a bird entered a travel cage but back-tracked into the patch cage it had just departed from, the time spent in the travel cage was excluded.

Statistical analysis

I compared data among treatments (solitary, with budgie, and with mannikin companions) by means of repeated measures ANOVA. When treatment had a significant effect on a particular variable, the results were further analysed according to whether the subject foraged in the patch cage that was adjacent to companions

or not. Subjects, therefore, could forage at five possible patch types: away from or with budgies, away from or with mannikins and solitarily (I considered both patches of the solitary treatment to be of the same type as the subjects showed no side preference in the apparatus). Finally, post-hoc multiple comparisons were conducted in both analyses by means of Bonferroni tests. When necessary, I inverse transformed data (1/x) to satisfy the ANOVA's assumptions. However, as the results using transformed data were not different from those using untransformed data, the figures referred to below are plots of the original untransformed data.

RESULTS

The eight subjects were observed over a total of 144 trials conducted during a period of 72 days yielding a total of 26 h of observations during which 1133 patches were exploited and 7143 seeds were consumed. The average trial lasted 651 ± 17s (s.e.) during which subjects exploited an average of 7.9 ± 0.2 (s.e.) patches and ate 50.0 ±1.3 seeds (s.e.).

Trial duration, seeds eaten and patches visited

The duration of trials was affected by treatment ($F_{2,7}$=5.58, P=0.02; Fig. 2) with trials in the solitary treatment being shorter that the others. The number of patches exploited per trial was significantly affected by treatment ($F_{2,7}$=8.1, P=0.005; Fig. 3). Subjects exploited significantly fewer patches in the conspecific trials than in solitary

trials while the number of patches exploited in the budgie treatment was intermediate and not significantly different from that recorded in the solitary and conspecific treatments.

The total number of seeds consumed during a trial was affected by treatment ($F_{2,7}$=9.67, P=0.002; Fig. 4). Subjects consumed fewer seeds during a conspecific trial than during any other. The number of seeds consumed during trials of the budgie treatment was not different from the number consumed during the solitary treatments. The number of seeds eaten per patch, however, was not affected by treatment ($F_{2,7}$=0.5, P=0.62) or by the proximity of companions ($F_{4,7}$=1.00, P=0.42). Given that the birds visited fewer patches in more time in the conspecific treatment while keeping the number of seeds eaten per patch constant, the overall feeding rate per trial was significantly affected by treatment: it was lowest in the conspecific treatment and highest in the solitary treatment ($F_{2,7}$=25.42, P<0.001; Fig. 5).

Patch cage, patch, and non-foraging times

The birds stayed significantly longer times in the patch cages of the conspecific treatment ($F_{2,7}$=20.76, P<0.001, inverse transformed data; Fig. 6, top). The treatment effect is mostly due to an increased perching time spent next to conspecific companions ($F_{4,7}$=12.16, P<0.001 inverse transformed data; Fig. 6, bottom). Post-hoc comparisons confirm that cage visits were longest in the cage adjacent to mannikin companions; there were no significant differences between any other patch types.

The patch time was also affected by treatment ($F_{2,7}$=5.23, P=0.02; Fig. 7, top). Birds in the conspecific treatment remained longer in patches and those in the solitary treatment had shorter patch times while the budgie treatment had intermediate patch times that were statistically indistinguishable from the other two treatments and so analysis of patch types revealed no effect ($F_{4,7}$=1.06, P=0.4; Fig. 7, bottom).

Non foraging time was affected by treatment ($F_{2,7}$=22.57, P<0.001, inverse transformed data, Fig. 8, top). It was highest in the mannikin companion treatment and lowest in the solitary treatment. On a patch type level, non-foraging time was longer near the mannikin flock than in any other patch cage while it was longer with budgie companions than when away from conspecifics or in the solitary treatments ($F_{4,7}$=21.27, P<0.001; Fig. 8, bottom). There as no significant difference near or away from budgies.

Pecking time was affected by treatment ($F_{2,7}$=15.61, P<0.001) entirely due to longer pecking times in the conspecific companion treatment. Treatment still affected pecking time at the patch type level ($F_{4,7}$=13.95, P<0.001). Pecking time was longest of all near conspecific companions and birds had more pecking time near budgie companions than away from them.

Scanning time, rate and direction

Scanning time ($F_{2,7}$=10.02, P<0.001; Fig. 9A) and scanning rate ($F_{2,7}$=13.72, P<0.001; Fig. 9B) were both strongly affected by treatment with the least scanning

observed in the conspecific companion treatment. Finer analysis showed that scanning time was lower when subjects foraged next to companions and lowest of all when next to conspecific companions ($F_{4,7}$=15.78, P<0.001; Fig. 9C). Post-hoc comparisons indicate that there was no significant difference in scanning time between birds foraging away from conspecific companions, alone, or with budgie companions. The longest scanning time was observed when subjects foraged away from budgie companions. When comparing the different patch types, scanning rate was affected in much the same way as scanning time: subjects scanned less frequently when foraging in patches with companions and least of all with conspecific companions ($F_{4,7}$=17.13, P<0.001; Fig. 9D). Scanning rate was indistinguishable when foraging away from conspecific or budgie companions and in the solitary treatment. Also, there were no significant differences between scanning rates when foraging away from conspecific companions and either patches in the budgie companion treatment.

Treatment did not affect the direction of scanning. The proportion of scans directed to the flock cage was unaffected by treatment ($F_{2,7}$=0.56, P=0.58), and the same holds for the proportion of scanning time devoted to each direction ($F_{2,7}$=0.58, P=0.57). Analysis by patch types confirms the lack of significant effect on scan direction whether analysed as frequency ($F_{4,7}$=1.68, P=0.2) or time ($F_{4,7}$=1.27, P=0.3) scanning. Scan duration was unaffected by treatment ($F_{2,7}$=1.34, P=0.24) or patch type ($F_{4,7}$=0.92, P=0.455). The duration of scans toward the flock cage was not affected by treatment ($F_{2,7}$=0.58, P=0.57) or patch type ($F_{4,7}$=0.24, P=0.91). It follows that duration of scans away from the flock cage was also unaffected.

Patch feeding and pecking rates

Treatment had no effect on the patch feeding rates whether compared among treatments ($F_{2,7}$=0.23, P=0.23; Fig. 10, top) or among patch types ($F_{4,7}$=0.82, P=0.52; Fig. 10, bottom). The pecking rate was affected by treatment ($F_{2,7}$=21.25, P<0.001; Fig. 11, top) with the lowest pecking rate observed in the conspecific companion treatment. This effect was obvious only when the birds fed adjacent to conspecific companions ($F_{4,7}$=18.67, P<0.001; Fig. 11, bottom). Post-hoc tests confirm that the pecking rate was lowest near conspecific companions but not statistically different whether subjects foraged away from conspecific or budgie companions, in the solitary treatment, or with budgie companions.

Travel times

Travel time was affected by treatment ($F_{2,7}$=7.02, P=0.024 (Huynh Feldt correction), Fig. 12, top) with subjects travelling more quickly in the conspecific treatment. Travel time was not significantly different in budgie or solitary treatments. Travel time was also affected by the type of patch that was exploited ($F_{4,7}$=4.93, P=0.029 (Huynh Feldt correction), Fig. 12, bottom). Subjects spent less time travelling to each patch in the conspecific treatment than to the patch adjacent to a flock of budgies.

DISCUSSION

My results confirm that, as was observed in starlings (Vasquez & Kacelnik 2000), nutmeg mannikins respond to the presence of non-feeding conspecifics at a

foraging site by altering their foraging rate independently of any change in access to the food. However, my study goes beyond the results obtained for starlings because the effects were observed almost exclusively in the vicinity of companions and occurred at two behavioural levels:1- an increase in non-foraging activity and 2- a reduction in foraging rate with conspecific companions that were equivalent to self-imposed interference. I discuss both levels of effects in turn.

Increased non-foraging activity

When the birds foraged in companion treatments they spent more non-foraging time adjacent to conspecific companions than when away from them, but this effect was non-significant with budgie companions. The subjects also took fewer seeds as a result of exploiting fewer patches but travelled significantly faster between patches. Despite these faster travel speeds, the birds in the conspecific companion treatment achieved the lowest feeding rates (40% lower than in the solitary treatment). By spending more non-foraging time in the patch cage, the subjects experienced lower patch encounter rates, and hence took longer to exploit 10 patches and often gave up foraging before the full 10 patches criterion had been reached. The lowered feeding rates can therefore be attributed primarily to the extra non-foraging time that subjects spent perched next to conspecific companions.

This extra time spent perched near conspecific companions may not be entirely surprising for such a social bird (Goodwin 1982, Immelman 1982). It implies that the birds were attempting to spend more time close to companions. However, in this context, it is noteworthy that the birds did this at some foraging costs and did

not opt to increase the time exploiting the patch, a behaviour that could also have maintained proximity to companions while attenuating its foraging rate cost. Instead the birds simply perched, apparently inactive, close to companions. It is the cost that this behaviour imposes in terms of reduced foraging rates that suggests it may be worth exploring whether the response is relevant to more natural foraging situations.

It is possible that subjects in my apparatus attempted to synchronize their foraging activity with the activity of the non-foraging mannikin companions. Such synchronization would be necessary to maintain flock cohesion (Birke 1974, Valone 1993). Perhaps in the conspecific companion treatment, once the subjects had exploited their patch they waited in the patch cage close to companions until the companions decided to exploit the next patch, something they could not do. This extra time, therefore could involve waiting or possibly even attempts to coax the flock to follow. Presumably, when birds forage together this non-foraging time would be reduced as all birds could leave to exploit patches together. However, this cost of maintaining flock cohesion may occur in natural circumstances when animals change groups. In this case it is conceivable that the individual that joins the group is unsynchronized; perhaps it is hungry when all others are satiated. My results suggest that in those cases individuals may have to pay a cost to maintain group cohesion.

Other studies have documented costs of flock cohesion. For instance, in a study of social patch exploitation conducted on the same species and in the same type of apparatus, the subjects foraged in trios at the same patch (Livoreil & Giraldeau 1997). Each trio's omega bird consistently exploited the patch less

extensively than others when foraging alone and so its optimal patch departure time came earlier than the optimal patch times of its partners. Yet, when the omega bird was in the trio it remained in the patch beyond its optimal emigration threshold as if it forfeited the maximization of its feeding rate in order to remain with the group members.

Reduced foraging rates have already been shown to have negative long-term consequences on reproductive success in another estridid finch the zebra finches (*Taeniopygia guttata*) (Lemon & Barth 1992). While experiencing experimentally reduced foraging rates in the order of 60% , zebra finches still consumed as much food as those foraging at higher rates. If rate reductions without reduction of intake lead to lower fitness, reduced total intakes coupled with lower feeding rates are almost certain to impose biologically significant fitness costs (Reznick 1985).

Vasquez and Kacelnik's (2000) starlings responded to the simulated presence of competitors by increasing the duration of the pre-response interval (the time between entry into the operant box to the first response to its feeder) as well as increasing their giving up time (the time between the last response and leaving the operant). These are equivalent to non-foraging time in as much as they do not involve responding at the operant. Despite these increases in non-foraging time near conspecifics, their subjects did not spend significantly more time in that operant box or have lower feeding rates. It is possible that the starlings pecked more quickly at the feeder near other starlings to compensate for this extra non-foraging time but the authors provide no data to support or

refute this.

Reallocating behaviour at the patch

The presence of companions affected details of patch exploitation behaviour that reduced the subjects' foraging rate. This result goes beyond those of Vasquez and Kacelnik (2000) because my birds were actually involved in exploiting a patch that required the bird to search for and handle each prey item before it could be ingested. As a result, my study shows that the presence of companions led to a commonly observed response in foraging groups: a reduction in the investment in scanning because the subjects reduced both their scanning time and their scanning rate (Lendrem 1984, Elgar 1989b, see Roberts 1996 for a review). This response suggests that the subjects reacted to the simulated presence of competitors as if group size had increased. However, neither the proportion of scans directed towards companions nor the proportion of scanning time oriented towards the companion cage were affected by treatment. So, when mannikins were present, the subjects lowered their overall level of scanning but did not alter the direction of their scans.

Generally, a reduction in scanning rate is concomitant with an increase in feeding rates; the so-called scanning group size effect (Pulliam 1973, Lima et al. 1999, Schmaltz ms). In contrast, I found no change in the patch feeding rate even though less patch time was devoted to scanning and search for seeds was less frequently interrupted for scanning. The absence of an increased feeding rate when less time is lost to scanning implies that seed pecking rates, which exclude time

used for scanning, declined in the presence of companions

The absence of an increased feeding rate in the presence of competitors could be the result of a purely proximate constraint. It is possible that the sight of non-foraging companions was a sufficient visual and auditory signal to allow the birds to respond by decreasing their scanning. However, the absence of feeding in these birds could have been an inappropriate signal to elicit a competitive feeding response. For instance, individual domestic chicks (*Gallus gallus domesticus*) (Tolman 1965, Tolman & Wilson 1965) do not change their pecking rate when they see a mirror image of themselves or a conspecific behind a transparent partition but increase it when a conspecific is placed in the same enclosure as the subject. If this is so in mannikins, the complete scanning-group size effect may have required the presence of companions that are also engaged in feeding, possibly even in the same holding cage or patch. The presence of non-feeding birds in an adjacent cage could provide the subjects with the cues necessary to reduce their scanning but not increase their pecking rate. This, however, would only explain why the pecking rate failed to increase and not why it actually decreased.

Another possible reason why the pecking rate did not increase is that the seeds were too easily available and did not require any search and therefore the pecking rate was limited by the handling time for each seed. This is unlikely because the same patch used in a similar study with the same species generated a significant increase in inter-peck intervals as the patch depleted (Livoreil & Giraldeau 1997). Also, if this were the case an increase in search time would certainly have lead to an increase in the number of seeds consumed and this was

not observed.

The lowered pecking rate may actually be due to the way I calculated it- by subtracting scanning time from total patch time. The birds commonly handle seeds while they scan. However, since they scan less in the presence of companions, some of the handling that normally occurs during scanning may have been conducted with the head down when in the presence of companions. This means that when the scans are removed from patch time, a greater portion of handling time may be included in pecking time when the animal was in the presence of competitors than when it was alone. This would obviously lead to a decreased pecking rate because some of the subject's search time would now be used for handling which probably could not be concomitant with moving peas to reach seeds.

Although possible, explanations invoking the handling of seeds while holding the head down seem improbable for the following reason. Subjects scanned an average of 10.6±0.6 times per patch visit while consuming 6.3±0.3 seeds when in the presence of conspecifics. Therefore, they scanned more frequently than would be expected on the basis of seed handling requirements. Also, scan duration was unaffected by the presence of companions and in studies where handling time is measured, this time tends to decrease when birds are in the presence of conspecifics (Glück 1987, Beauchamp & Livoreil 1997 using nutmeg mannikins), possibly to partake in a larger share of the food resources. Therefore, there is no reason to assume subjects spent more time handling seeds with their heads down near conspecifics because they scanned less.

Assuming that the birds continued to do all their handling while scanning

even in the conspecific treatment, then the decline in pecking rate observed when the bird feeds next to conspecific companions fits the broadest definition of interference (Goss-Custard 1980) as it corresponds to an immediate and seemingly reversible decrease in feeding rate in the presence of companions. It follows that the presence of companions has interference-like consequences even in the absence of any physical interaction between subject and companions. Interference-like effects have been obsered in the absence of any overt behavioural change between competitors. In ground-feeding *T. merula*, an individual's feeding rate is lower in the presence of companions and this inhibiting effect is similar whether or not there are aggressive interactions between birds (Creswell 1997). Thez interference noted in *T. merula* is attributed to the birds' monitoring one another while searching for food which prevents the birds from benefitting from reduced scanning because they must maintain significant attention directed to potential competitors (Creswell 1997). Juncos (*Junco hyemalis*) searching for food on the ground with their heads down can apparently detect movement and are thus capable of low quality vigilance for aerial predators (Lima & Bednekoff 1999). It is possible that in my case when the mannikins foraged with conspecifics that they replaced their higher quality scanning vigilance by some lower quality vigilance that occurred while they searched and handled seeds.

To date, a number of other studies have confirmed the effects of competitors on foraging behaviour by using simulated competitor presence or apparent sociality. Shrews (*Sorex araneus*) increase their foraging rate and intake when the site, odour

and sound of an apparent competitor is detected but the subjects' rise in activity also increases their metabolic rate (Barnard et al. 1983). Willow tits (*Parus montana*) repeatedly choose a small prey item near an empty cage over a large prey item near a cage containing a dominant conspecific (Trandem & Lampe 1993). Finally, starlings feed more quickly at a patch that is located away from competitors than the patch close to competitors, travel faster when moving towards a patch with conspecifics and take longer to start foraging when they enter the patch and longer to leave the patch when foraging is finished when in the patch adjacent to conspecific foragers (Vasquez & Kacelnik 2000). All these studies show that social animals experience self imposed changes to their foraging behaviour when foraging in the presence of companions.

Effects of heterospecifics

In four cases (feeding rate per trial, patch time, non-foraging time, and scan rate) the budgie companion treatment elicited a response that was intermediate and significantly different from the other two treatments. In three of these (patch time, non-foraging time and scan rate) these effects disappeared when the data was analysed by patch type. In the fourth case (feeding rate per trial) the observed effect was due to a behaviour subjects did not perform in other treatments. When encountering a budgie flock the subjects tended to perch in the doorway to the feeding cage for a few seconds before proceeding to the food patch. As this did not occur in other treatments I did not feel it was something I should analyse in the

same way as other data I recorded.

This last effect appears to be due to the species chosen as heterospecific companion. Perhaps the size of the companions intimidated the subject at first site. While Vasquez & Kacelnik (2000) chose companions that were much smaller than the subjects to avoid such concerns, it was not feasible to do this as the mannikins are already rather small. Choosing heterospecifics of similar size to the mannikins was a concern because the subjects had previously existed in a population composed of zebra finches and society finches (*Lonchura striata*) as well other mannikins and therefore other small bird companions may have elicited the same response as mannikin companions. In that case it would have been impossible to attribute the responses exclusively to the presence of conspecifics. Budgies were selected because they are social, granivorous birds that the subjects were unlikely to encounter in the wild and were not familiar with in captivity. The two species did not appear to be aggressive toward one another. I conclude that because the budgies did not cause responses where conspecifics did- including scanning behaviour- they were a good choice of a neutral companion species.

CONCLUSION

My study confirms that the presence of companions causes individuals to increase their travel speed between patches when conspecifics are present. The major effect of companions is the addition of a significant portion of non-foraging time in the patch adjacent to conspecific companions that reduced the animal's overall foraging

rate. However, companions did lead to a reduced scanning investment but no concomitant increase in feeding rate. Unlike results obtained by Vasquez and Kacelnik (2000), the effects reported here occur mostly while the animal forages in the patch adjacent to conspecifics. This point does not exclude the possibility that the effects occurring in my system also operated on the starlings used by Vasquez and Kacelnik (2000). Yet these could not be detected due to the way data was recorded (no direct observations), how different areas of the apparatus were defined (food patches), and how some behaviour patterns were measured (travel included the giving up time at one feeder and the pre-response time at the following feeder).

I may have uncovered a hidden social foraging cost at different behavioural levels. While I can confirm a cost due to an increase in non-foraging activity, the current results indicate there may be a cost during the actual food search. My work has shown, however, the importance of direct behavioural observation in the study of patch exploitation as this led to the discovery of a group size effect without an increase in feeding rate. This result in itself has raised the question of exactly why this happened. Was it due to my apparatus and testing conditions? If so, I may have dissected the cues responsible for the group size effect. Was it because birds increased their handling times? This could show another effect of sociality on the tradeoff between digestive cost and feeding rate (Sibly 1981, Kenward & Sibly 1977). Are nutmeg mannikins suffering the costs of interference solely caused by the presence of conspecifics? These are questions that should be answered by similar studies that focus on handling times (Johnson et al. in press).

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FIGURE CAPTIONS

Figure 1. Top view of the apparatus. e: opening through which subjects entered the apparatus. f: flock cage. p: food patch. s: slit though which food patch was replaced. t: tinted plexiglass. The bold line represents the opaque blind.

Figure 2. Trial duration per treatment. Bars represent, from left to right, budgie companion treatment, solitary treatment, and conspecific treatment. Letters on bars indicate significant differences between means (±s.e.). (Bonferroni test α=0.05).

Figure 3. Patches exploited per trial. Legend as in Figure 2. (Bonferroni test α=0.05).

Figure 4. Seeds consumed per trial. Legend as in Figure 2. (Bonferroni test α=0.05).

Figure 5. Feeding rate per treatment. Legend as in Figure 2. (Bonferroni test α=0.05).

Figure 6. Patch cage times. Upper graph bars represent, from left to right, budgie companion treatment, solitary treatment, and conspecific treatment. Lower

graph bars represent, from left to right, away from budgie companions, with budgie companions, patches in the solitary treatment, away from conspecifics and with conspecifics. Letters on bars indicate significant differences between means (±s.e.). (Bonferroni test α=0.05).

Figure 7. Patch times. Legend as in Figure 6. (Bonferroni test α=0.05).

Figure 8. Non-foraging times. Legend as in Figure 6. (Bonferroni test α=0.05).

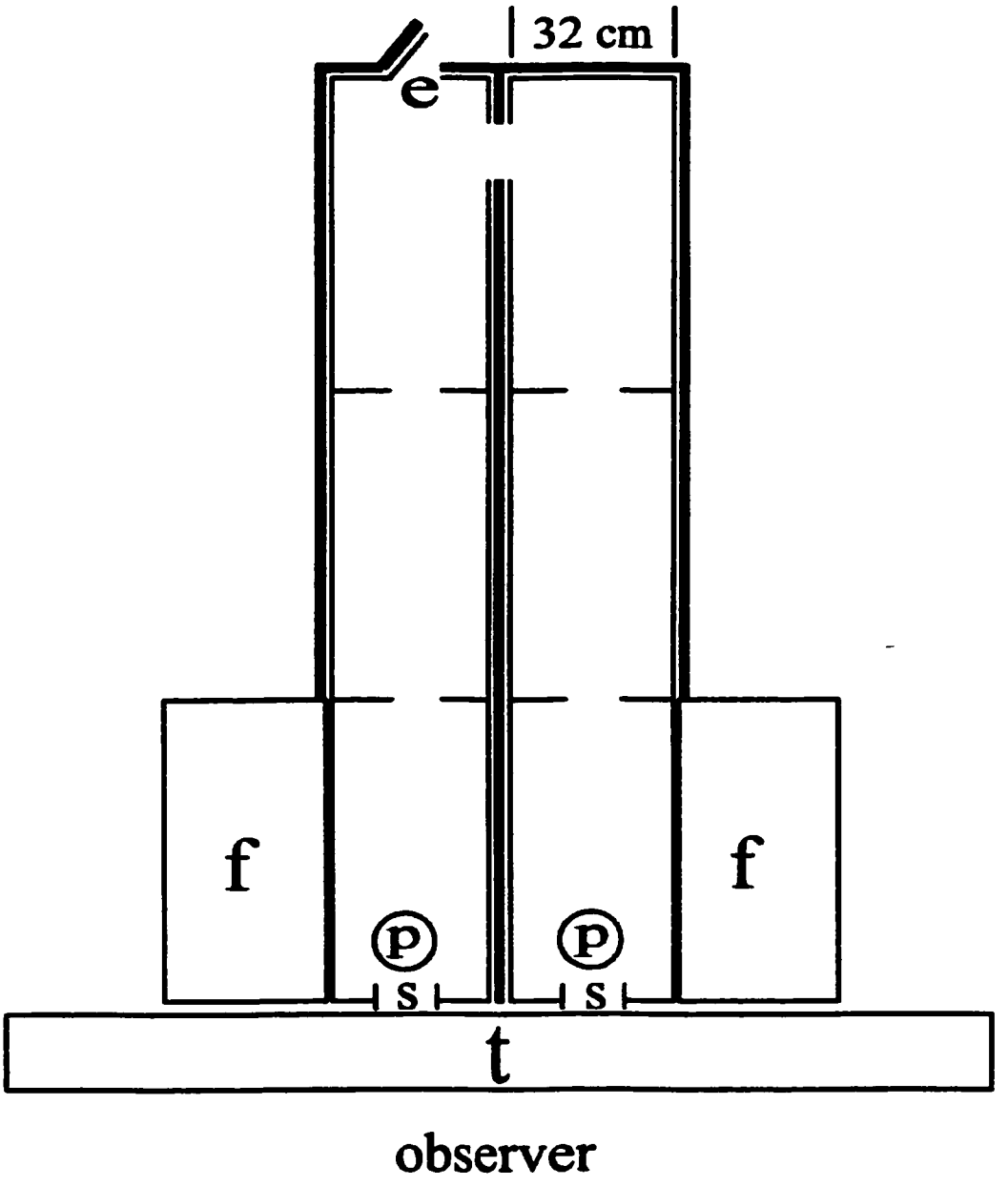
Figure 9. Scanning times and rates. A and C) Scanning times. B and D) Scanning rates. Legend as in Figure 6. (Bonferroni test α=0.05).

Figure 10. Patch feeding rates. Legends as in Figure 6. (Bonferroni test α=0.05).

Figure 11. Pecking rates. Legend as in Figure 6. (Bonferroni test α=0.05).

Figure 12. Travel times. Legend as in Figure 6. (Bonferroni test α=0.05).

Figure 1



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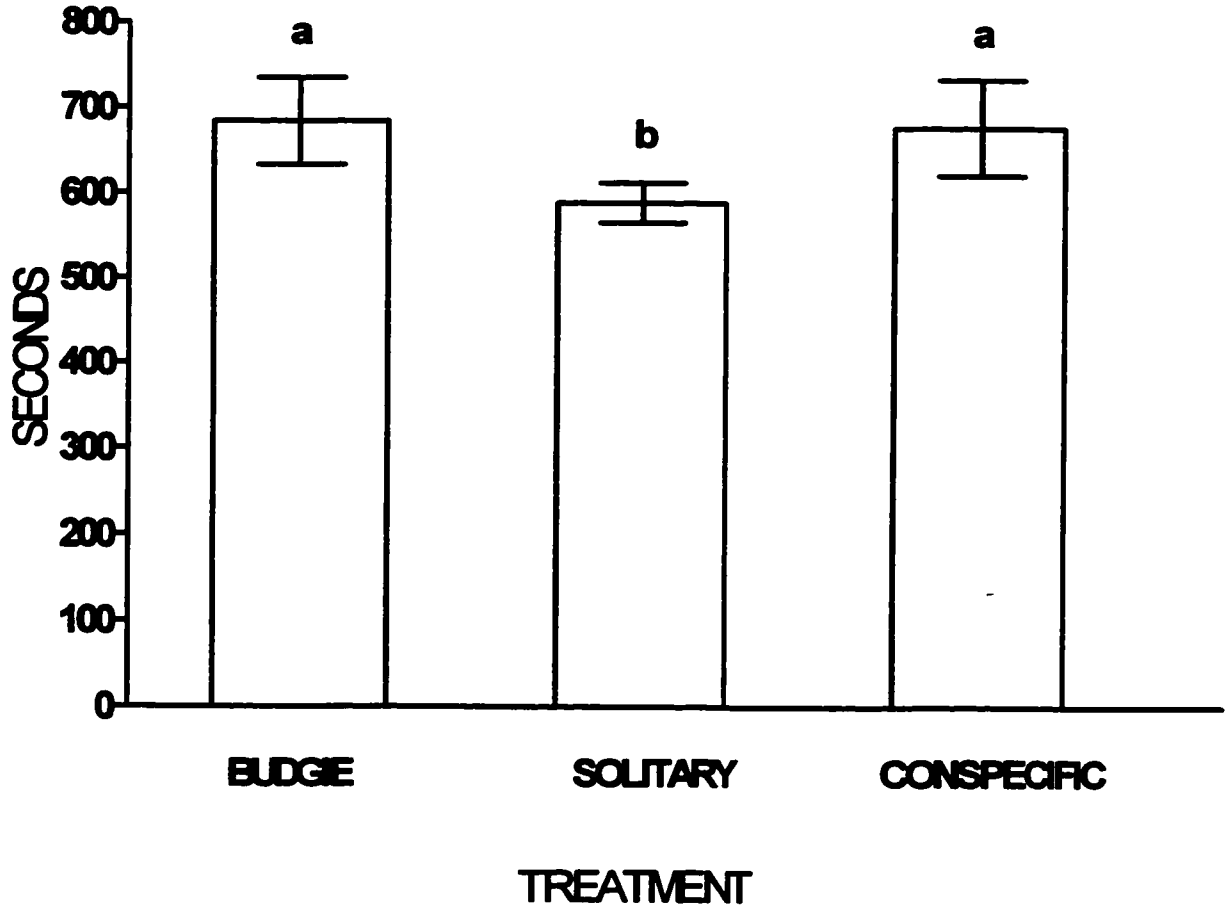
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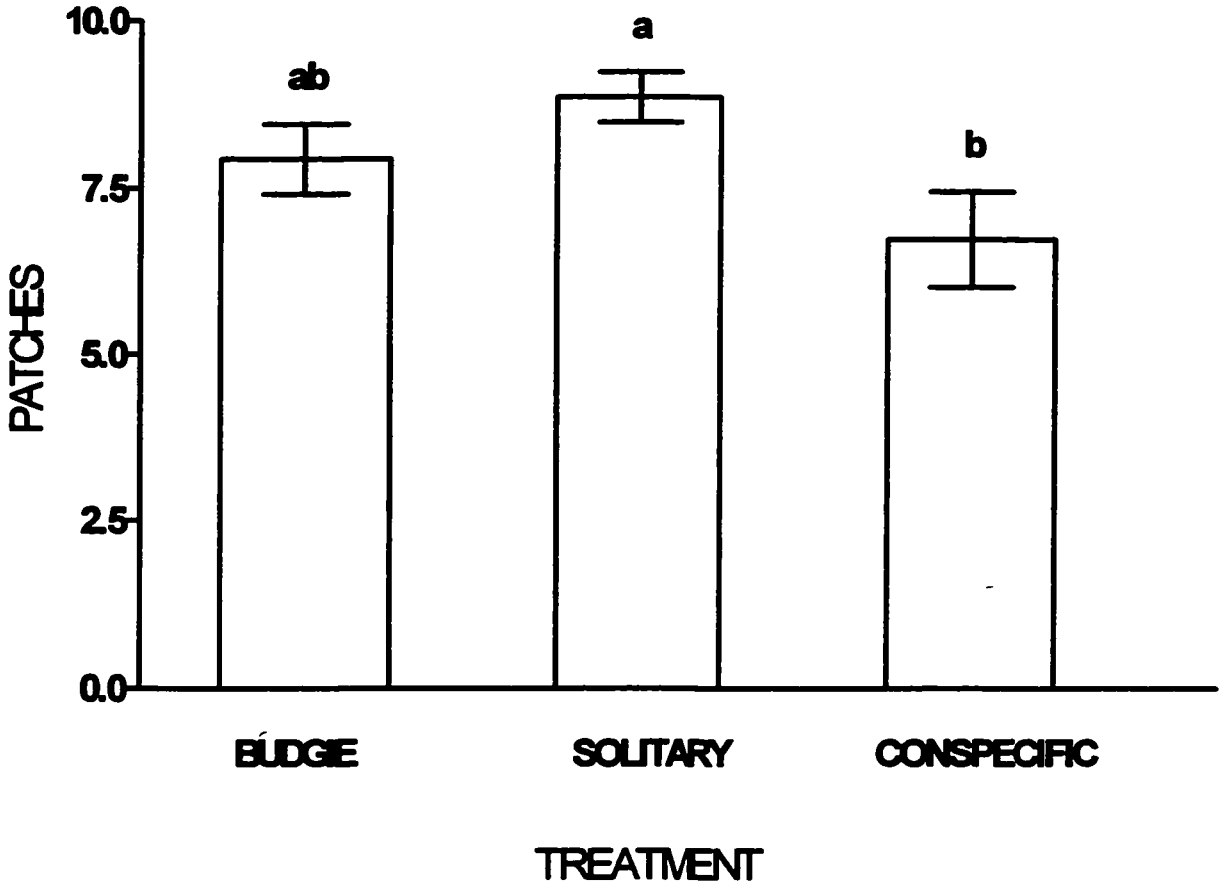
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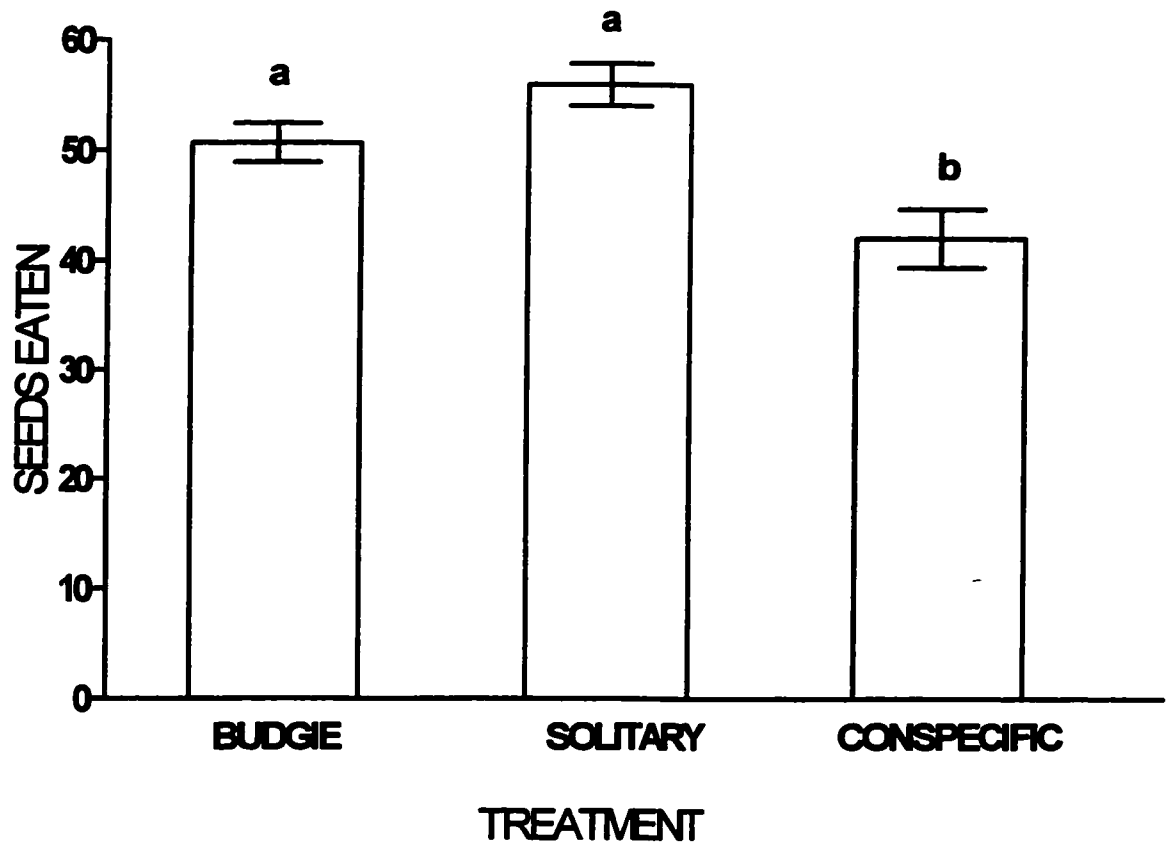
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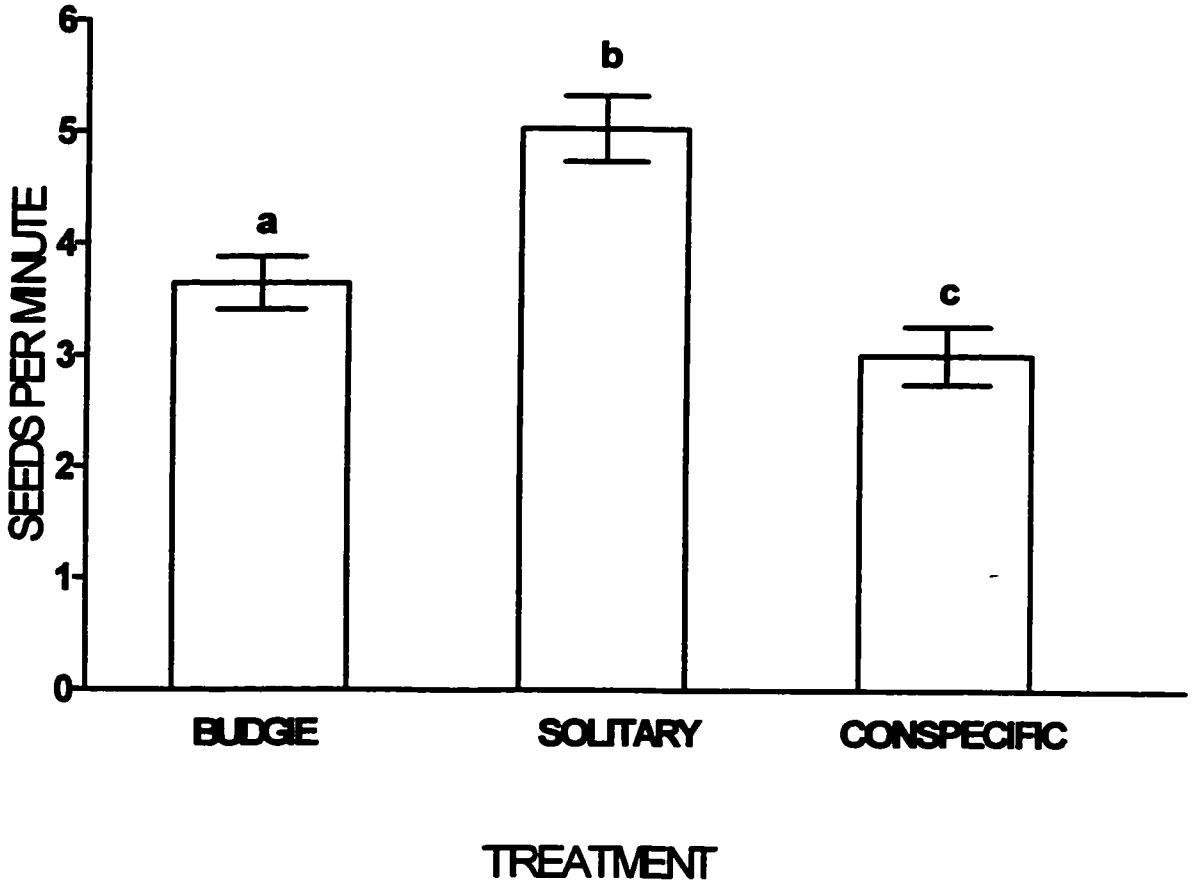
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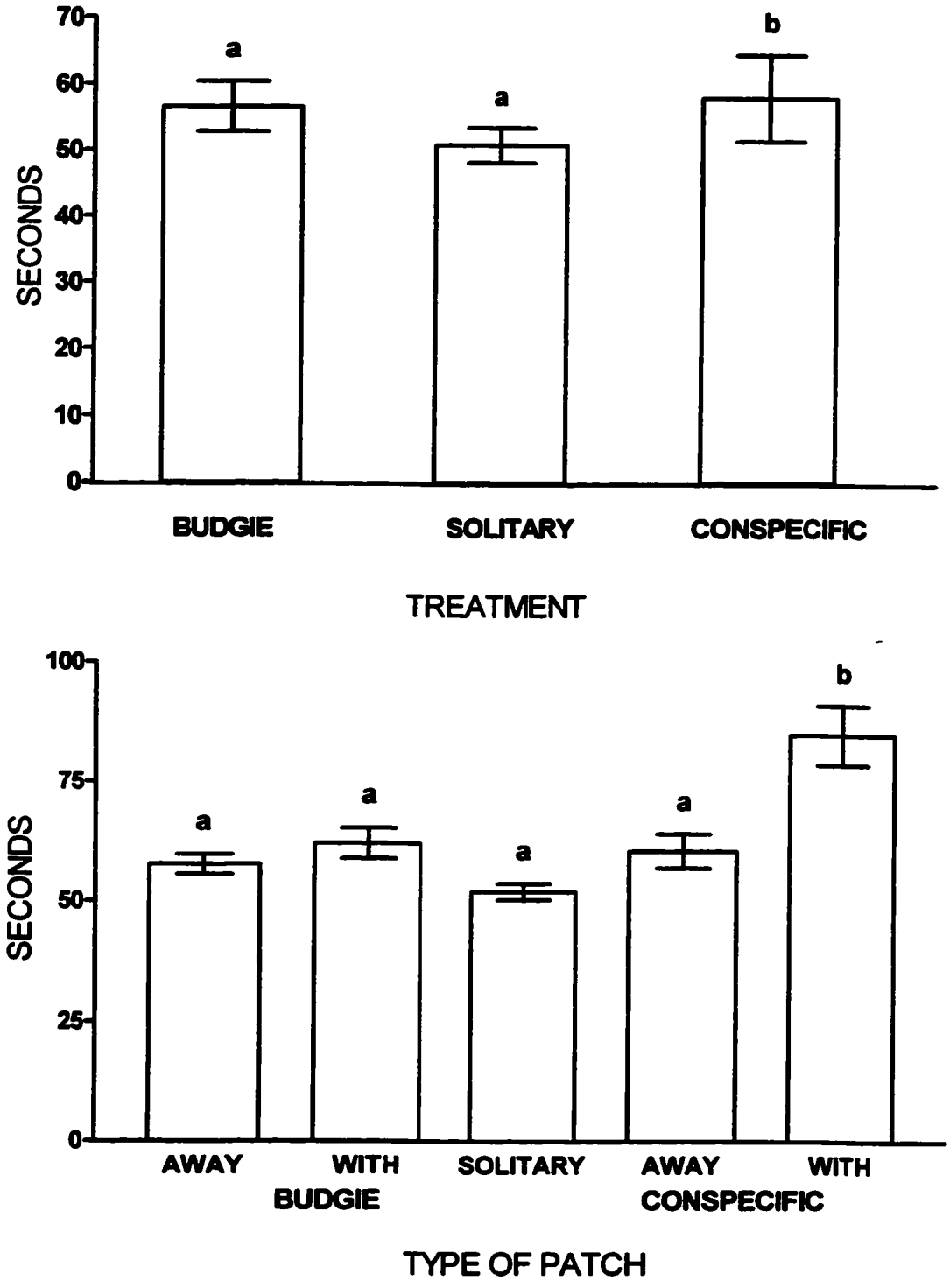
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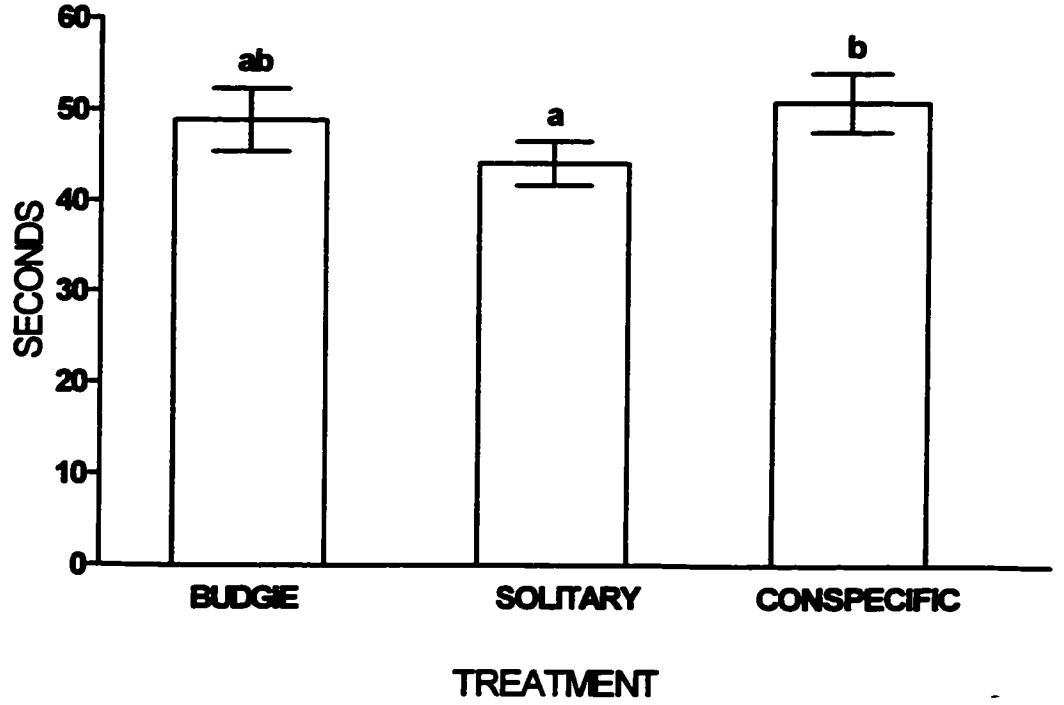
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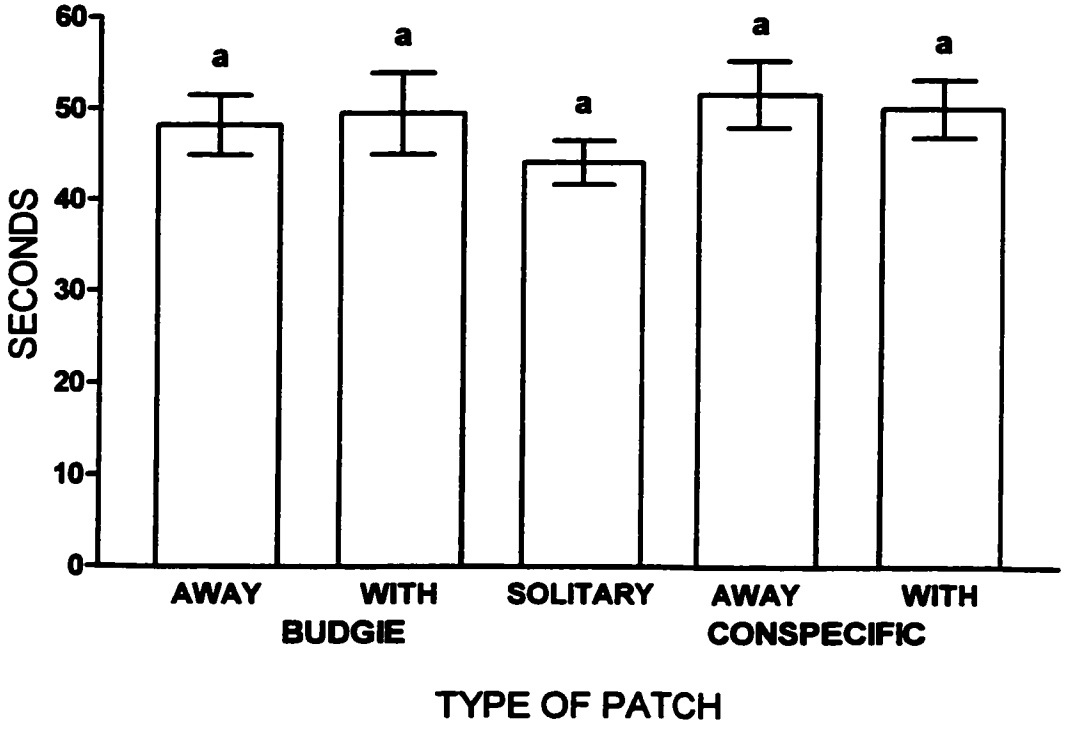
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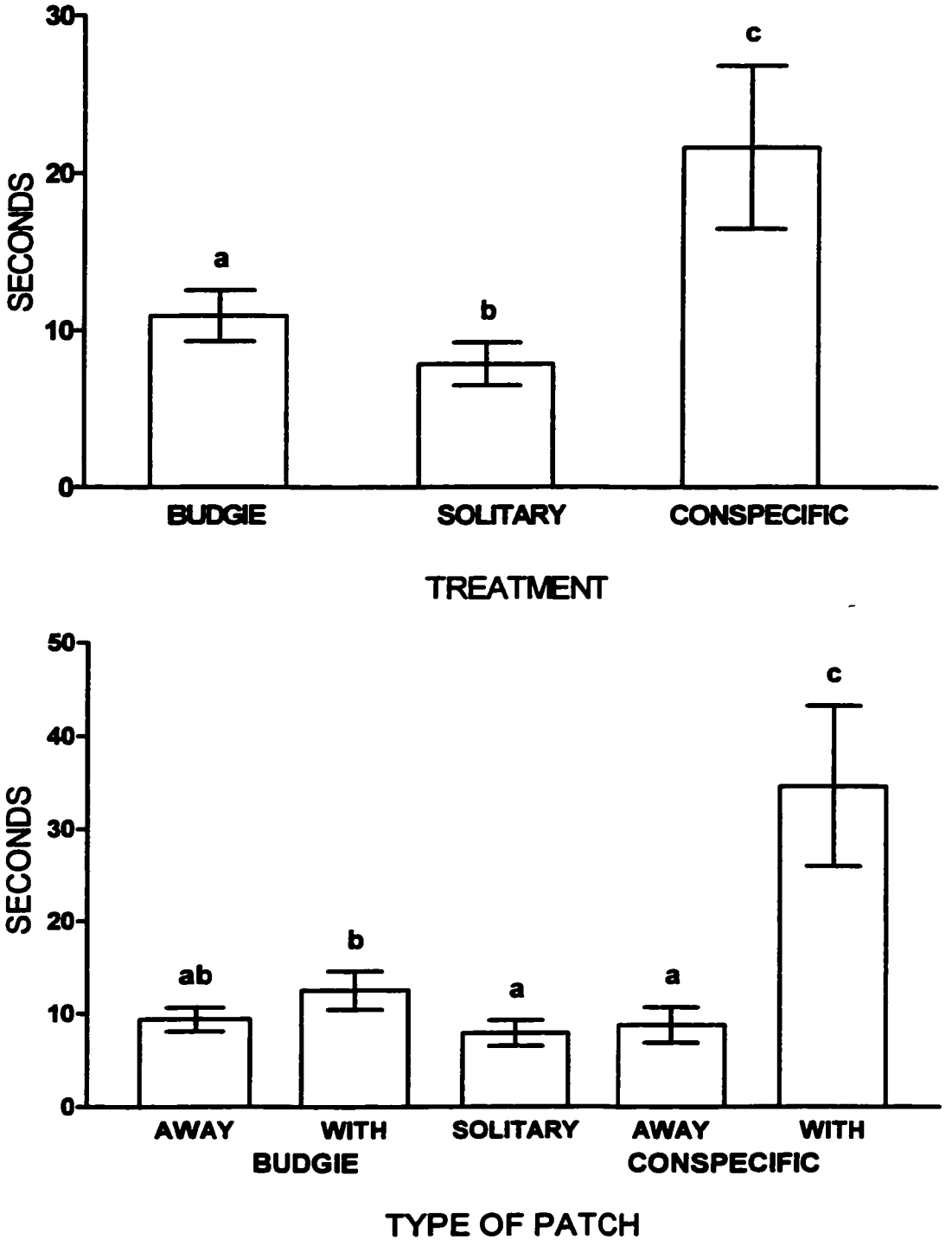
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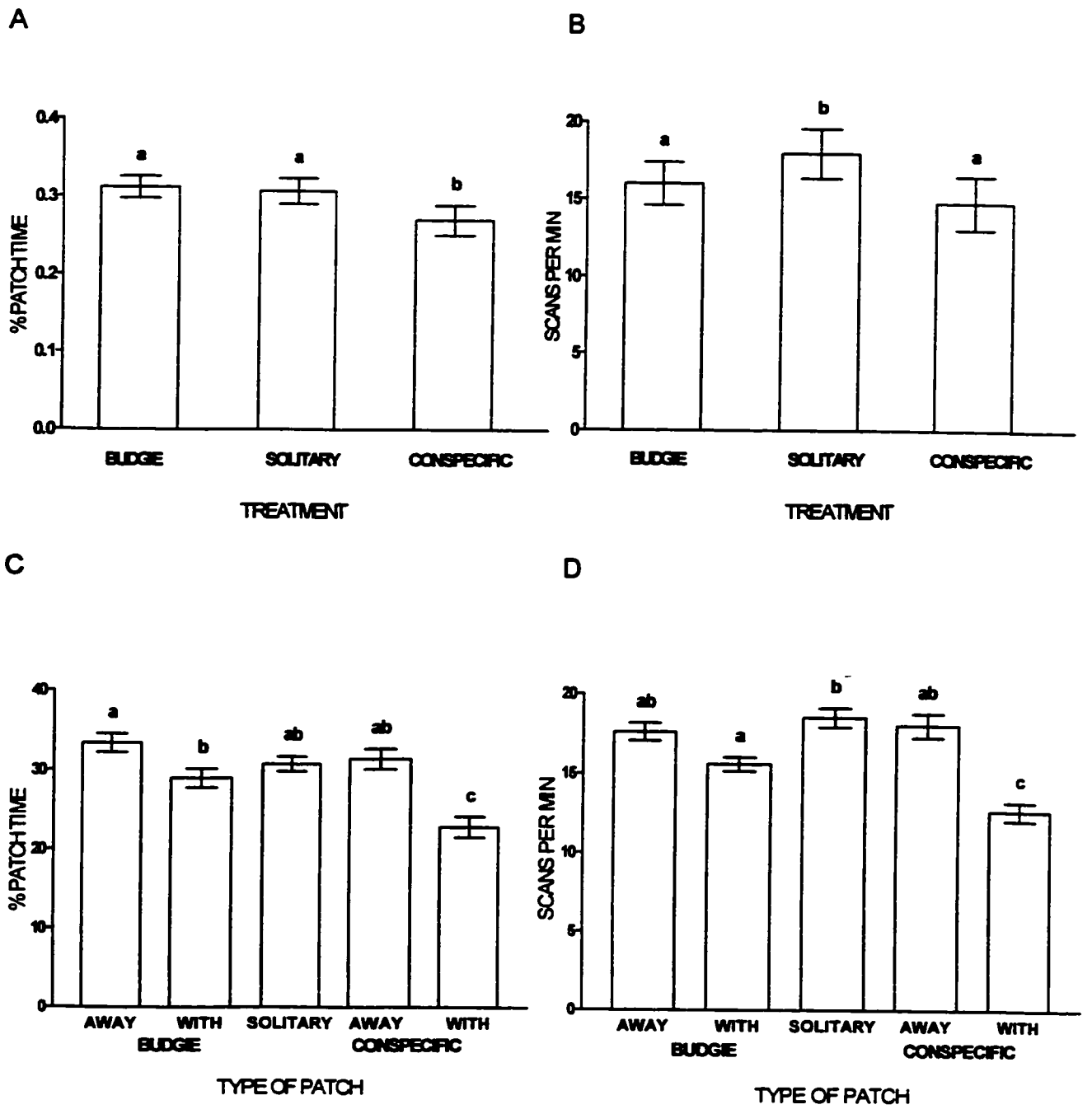
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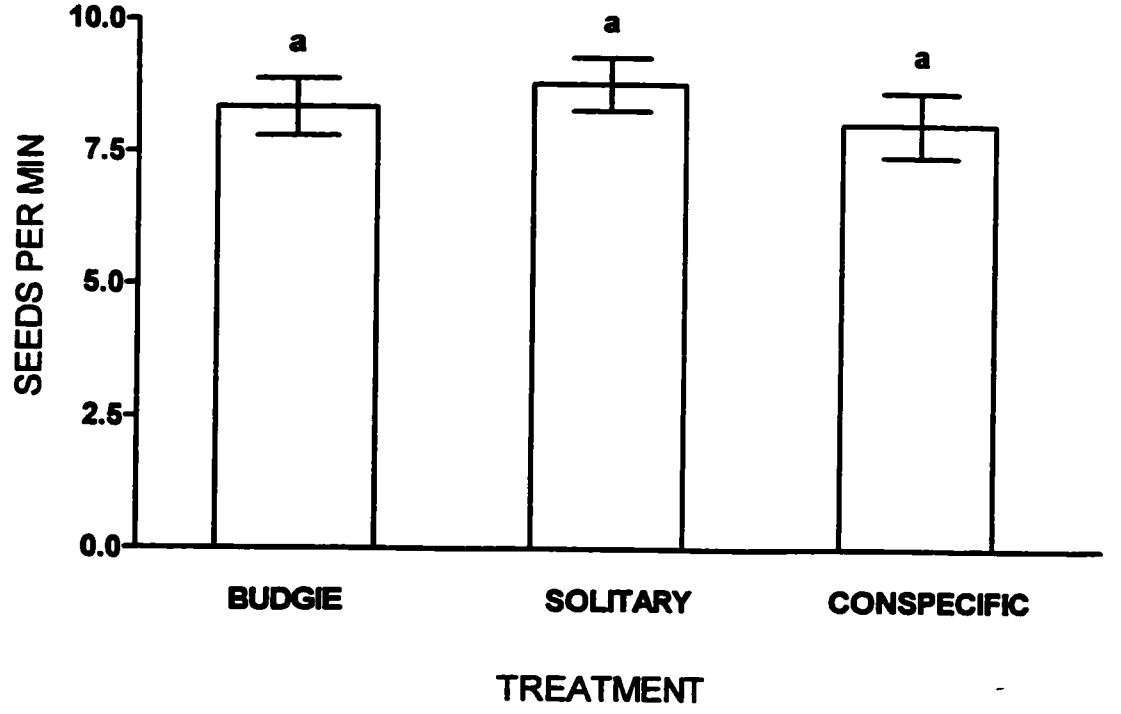
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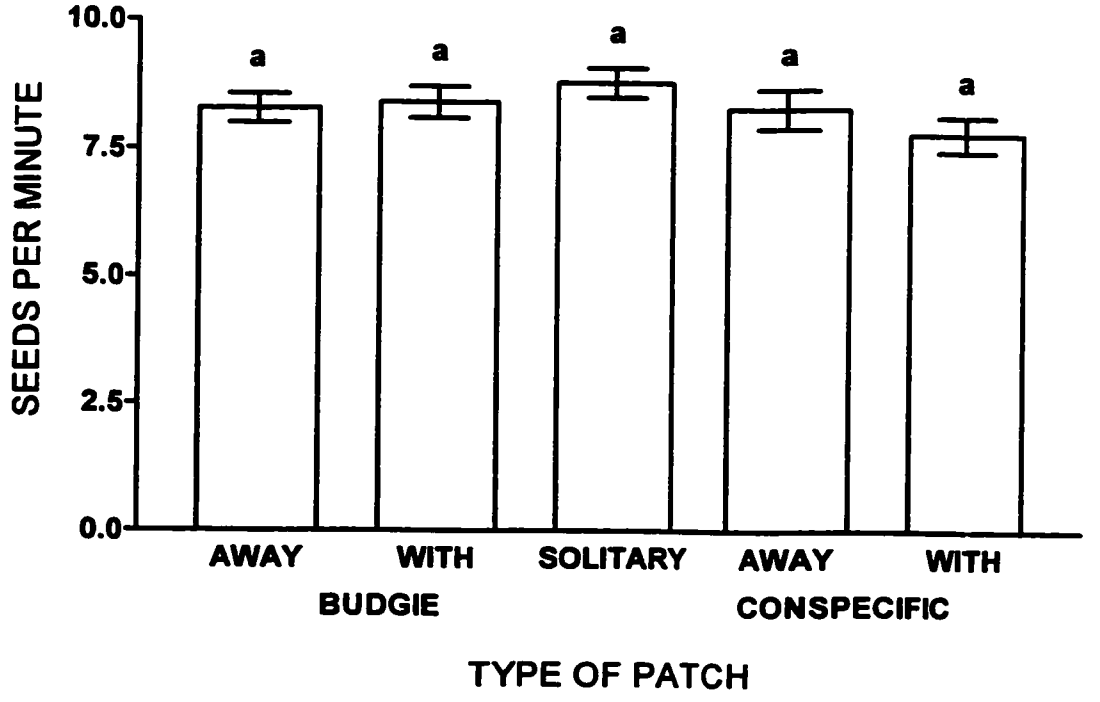
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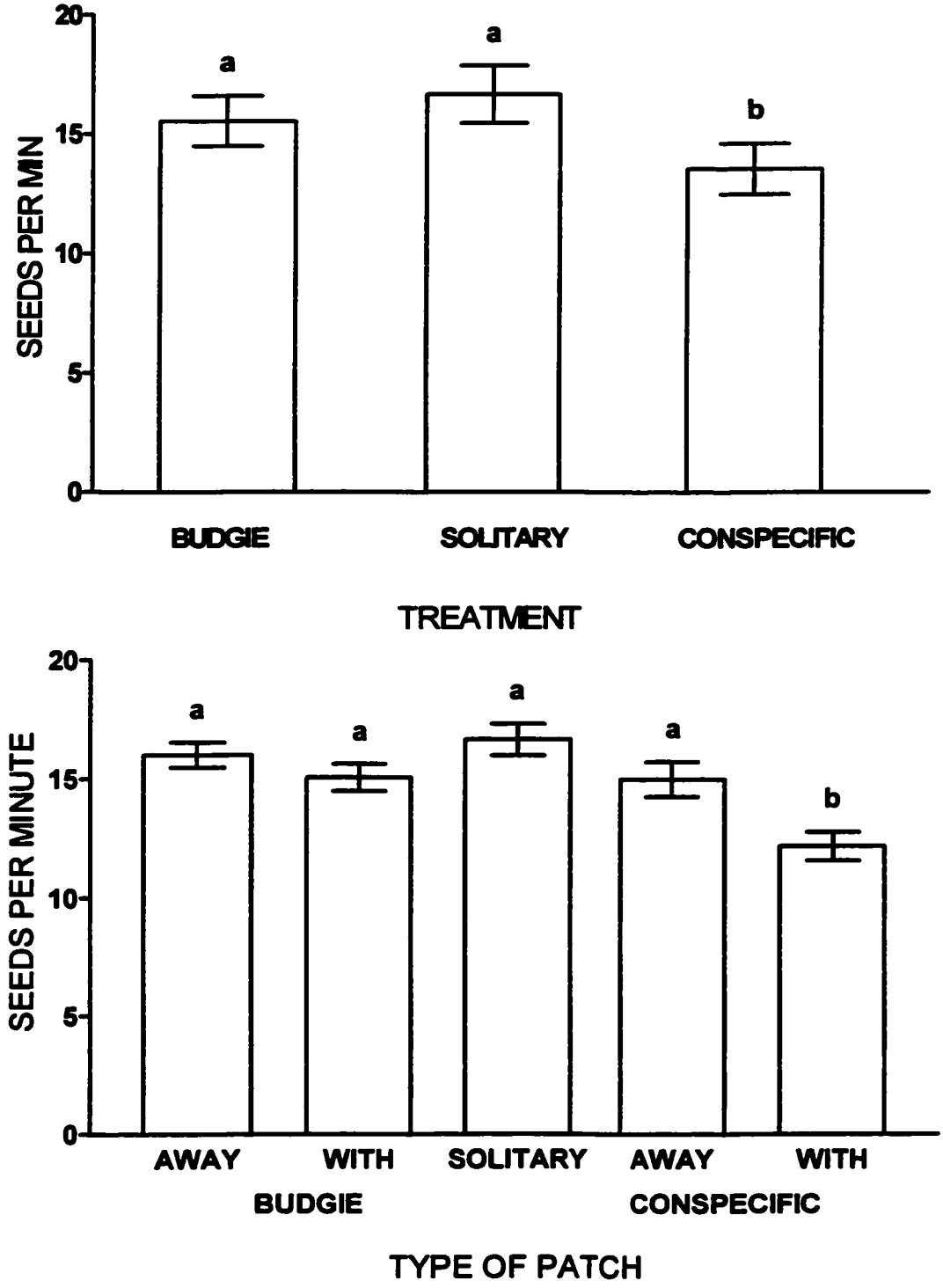
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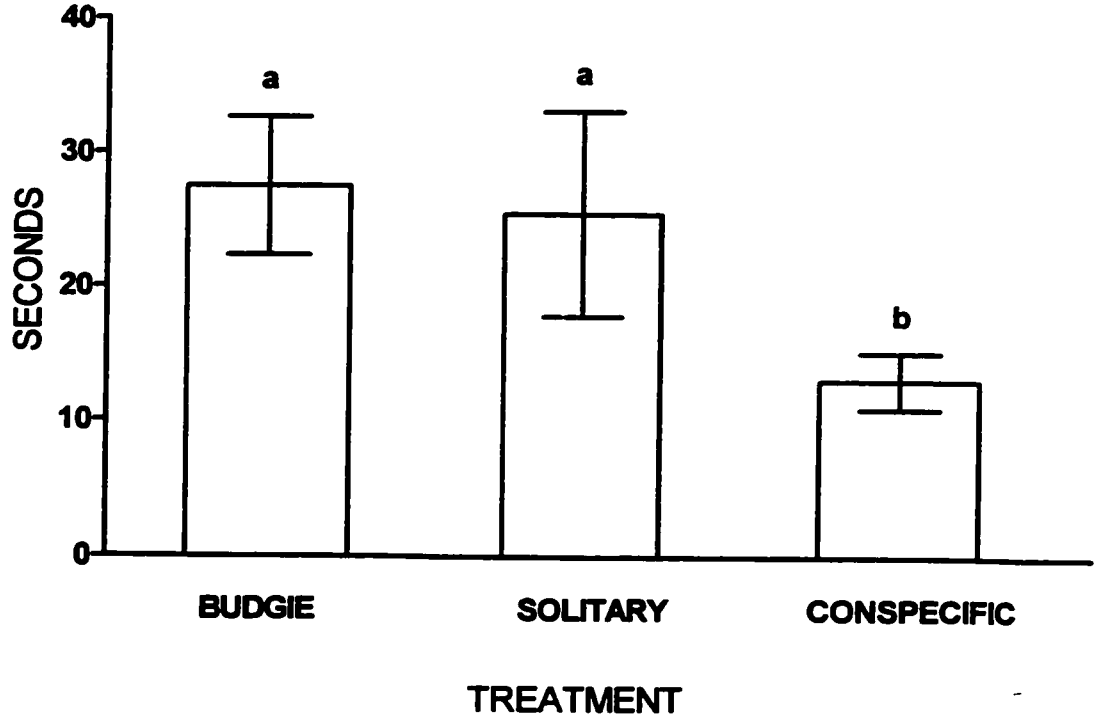
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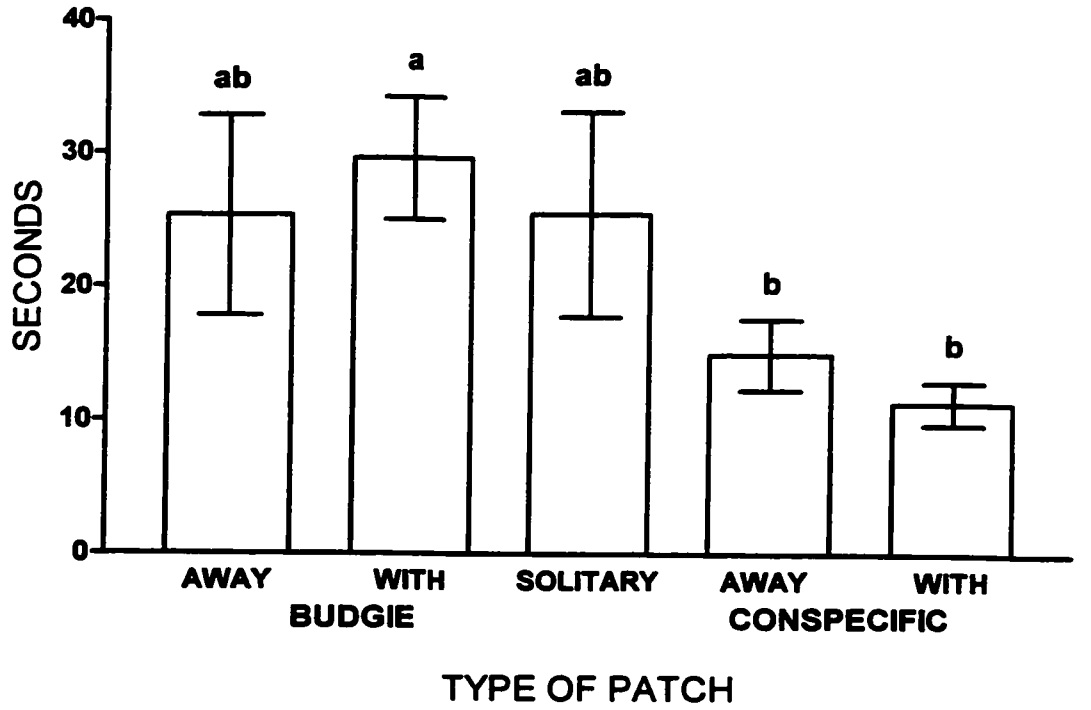
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