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November 2004

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Foraging patterns of male *Tiaris olivacea* (Yellow-Faced Grassquits) in different flock sizes

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ABSTRACT

Flock sizes can have both positive and negative consequences on foraging time of birds. It has been shown that increased flock size decreases any given bird's time spent scanning for predators and will allow them to increase their foraging time. In this paper I study male *Tiaris olivacea* (Yellow-faced Grassquits) in different flock sizes in the San Luis Valley, Puntarenas, Costa Rica. A total of 21 groups of *T. olivacea* were recorded in sizes of 1-50. No significant correlation was found between group size and time spent foraging by males when all data points were analyzed ($p = 0.0553$, $R^2 = 0.18$), but when an outlier point was removed (group size = 50), a significant positive correlation was found ($p = 0.0045$, $R^2 = 0.3685$). It appears that an increase in group size benefits male *T. olivacea* because it reduces the time they must spend scanning for predators and increases foraging time.

RESUMEN

El tamaño de una bandada puede tener consecuencias positivas y negativas sobre el tiempo del forrajeo de las aves. Se ha demostrado que conforme el tamaño de la bandada disminuye el tiempo que cada ave pasa vigilando disminuye y esto le permite aumentar el tiempo que emplea alimentándose. Se estudió a los machos del semillerito cariamarillo (*Tiaris olivacea)* en grupos de diferentes tamaños en el valle de San Luis, Puntarenas, Costa Rica. Un total de 21 grupos fueron registradas en tamaños que variaban entre 1 y 50 individuos. No se encontró ninguna correlación significativa entre el tamaño de los grupos y el tiempo del forrajeo de los machos cuando todos los datos fueron analizados ($p = 0.0553$, $R^2 = 0.18$); sin embargo cuando un dato extraordinario fue eliminado (Tamaño de los grupos = 50) la correlación fue significativa ($p = 0.0045$, $R^2 = 0.3685$). Parece que un aumento de tamaño del grupo ofrece una ventaja al *T. olivacea* macho, puesto que reduce el tiempo que se debe pasar vigilando y le permite aumentar el tiempo que emplea alimentándose. Entre las posibles razones para el dato extraordinario se incluyen la carencia de datos en grupos de tamaños similares y el hecho de que la amimentacion alcanza una asíntota a cierto tamaño de grupo.

INTRODUCTION

Flocking is an essential behavioral adaptation found in many bird species. When disrupted, social dysfunction can result, causing populations to fall to low densities, increasing its vulnerability of extinction (Gardner 2004). Reasons behind flocking behavior are numerous and include nest defense (Olendorf 2004), courtship, and mate attraction (Foster 1985). Two of the most important environmental influences that affect flock size are predators and food (Krebs and Davies 1981). Foraging time and predator surveillance come at a trade off for birds: A bird benefits from time spend feeding, but must also spend time scanning and surveying for predators. In other words, if a bird doesn't spend time feeding it will die of starvation and if a bird doesn't spend time scanning it will die of predation.

For many birds, individual predation surveillance time is reduced as a flock increases in size. Birds must scan and be alert for predators, but with an increase flock size, each individual can spend less of its own time scanning (Krebs and Davies 1981). In addition, it was found in ostriches that while each bird in a flock spends less time scanning, the overall scanning of a group increases with group size (Krebs and Davies 1981).

Because a bird's scanning time is reduced in larger flocks, it is generally thought that a bird has more time available for foraging (Krebs and Davies 1981; Krebs and Inman 1994). Flock sizes have been found to be smaller where predation is less prevalent (Beauchamp 2004), suggesting a correlation between larger flock size and increased defense against predation. Chen and Hsieh (2002) found that in mixed foraging flocks with the Grey-cheeked Fulvetta, larger flock size allowed birds to allot less time to scanning for predators and spend more time foraging.

However, in some bird species, such as juvenile rooks (Hart 1991) and male wintering diving ducks (Alexander 1987), as flock size increases, the number of antagonistic interactions among individuals has been shown to increase, taking away time a bird could use for foraging or reduce the rate at which they feed and thus make flock foraging less efficient for them (Hart 1991). Additionally studies of redshanks (Cresswell 1994) and ruddy turnstones (Fleischer 1983) show that, while an increase in flock size does reduce predation mortality, foraging benefits did not increase (Cresswell 1994; Fleischer 1983).

While foraging and predation cost/benefit patterns have been greatly studied in temperate areas, fewer studies have been done observing tropical birds. To examine how an increase in flock size affects predator scanning and foraging time in the tropics, I studied the neotropical finch, *Tiaris olivacea* (Yellow-faced grassquit). Although a fairly common species occurring from Florida and Mexico to Colombia and Venezuela (Ridgely 1981), *T. olivacea* behavior has been little studied. *Tiaris olivacea* individuals are known to forage in various flock sizes ranging from one bird to many (pers. obs.; Stiles and Skutch 1989), making it an ideal species for studying how predator defense and foraging behavior change with flock size. I focused my study on males within *T. olivacea* populations and hypothesized that in larger flocks, males would forage for more time than in smaller flocks because they would have to dedicate less of their own time to scanning. I also hypothesized that because their food resource, grass seeds, is abundant, antagonistic interactions for food would be reduced (Krebs and Davies 1981), and would not significantly decrease foraging time. Additionally, due to the lack of literature on *T. olivacea*, I made qualitative observations on patterns and trends I observed throughout the duration of my study.

MATERIALS AND METHODS

Study site

Research was conducted in pastures and roadsides of the San Luis Valley, Puntarenas, Costa Rica (Tropical Premontane Moist, Holdridge Life Zone 1, Fogden 1993). The area was divided into four microhabitats: forest, grassy open, tree in grassy open or near roadside, and tree patch near grassy open or roadside.

Data collection

Observations were taken during the non-breeding season (Stiles and Skutch 1989), from October 23, 2004 to November 15, 2004, between the hours of 8:00 AM and 1:00 PM. Flocks of *T. olivacea* were initially located either visually or by their call. Once a flock was found, its size and sex ratio were recorded, as well as its microhabitat type. Start and stop time of observations were also recorded.

One male in a flock was selected as the main subject of observation (males were distinguished from females based on morphological differences). Time spent foraging versus time not foraging for the male was recorded. Foraging was defined as time spent directly feeding, obtaining food, or in the foraging area unseen (e.g. if a bird was temporarily hidden by grass stalks). During non-foraging, three different actions of birds were recognized: perching, scanning for predators, and calling. Perching was defined as sitting, with little other movement. Scanning was defined as active surveying of the surroundings. Calling was defined as singing or otherwise vocalizing.

Any bird or flock of birds observed for fewer than three and a half minutes were excluded. An "observed" bird refers to one for which a data set was collected, while a "sighted" bird refers to birds seen but not observed long enough to collect data. An observation was considered finished when a bird or a flock was out of site for more than six consecutive minutes. If a bird did not return after six minutes, stop time of the observation was taken to be the last time the bird was seen. Other observational data about bird and flock behavior was noted as well including group behavior and male foraging patterns compared to female ones.

RESULTS

Quantitative

Observations of 21 flocks were collected in grassy open areas without any trees (two observations), at single trees (nine observations), and at tree patches (10 observations) next to grassy areas. Birds were never sighted in a forested microhabitat.

Maximum observation time was 31 minutes 34 minutes for a flock size of 50 individuals followed by 20 minutes 38 seconds for a male and female pair. Minimum time was 3 minutes 43seconds for a flock of one male and two females. Average observation time was 12 minutes 18 seconds (± 6 min. 41 sec.; Fig. 1)

No significant correlation was found between percent of time spent foraging and flock size (Fig. 2a, $p = 0.0553$, $R^2 = 0.18$, $n = 21$). However, the bird flock of 50 individuals was an outlier among the set because it was more than two times larger than the next largest group ($n = 21$). When taken out of the data set, the correlation between foraging time and flock size was significant (Fig 2b, $p = 0.0045$, $R^2 = 0.3685$).

The relationship between percent feeding time and number of males was also not significant (Fig. 3a, $p = 0.0707$, $R^2 = 0.1617$) but when the outlier datum was excluded, a significance difference was found (Fig. 3b, $p = 0.0227$, $R^2 = 0.2563$). Sex composition of each observation is shown in Table 1. There was no significant correlation between the sex ratio of a flock and its size ($p = 0.8124$, $R^2 = 0.0246$).

Qualitative

All birds that were observed feeding exhibited a similar "sally-like" behavior. This behavior consisted of an extended period of perching, in which the bird would also scan and call. The bird would then fly down into a grassy area and begin to feed. Scanning often occurred intermittently while foraging in the grass, but birds rarely called while foraging. After feeding, the bird would fly to a perch, often returning the same one, and the cycle would repeat. While recording individual sally times was not the focus of this study, three sally times for both a solitary male and a flock of nine are shown in Table 2.

Males were never observed interacting in antagonistic ways such as fighting for resources or quarrelling over females. Males were commonly observed alone, but a solitary female and a pair of females were observed only once each within the study. Birds were less commonly seen on very hot or windy days (No birds were seen or observed on extremely windy days, and only one group of inactive birds was seen on a hot day.). Cloud cover, mist, or light rain did not seem to limit bird activity. During the course of this study, no predatory birds or animals *T. olivacea* were seen.

Many solitary males appeared to have small or overlapping territories and oftentimes, when one of the males in this non-flocking group called, another would often call directly afterward. In male/female pairs, the male always foraged for equal or less time than the female. The male would remain perched while the female foraged in a grassy area below.

As group size increased, three different behavioral patterns appeared. First, fewer individuals were observed perching at any given time, and in the flocks of 16, 21, and 50 birds, there were periods when all individuals were foraging. Second, birds took turns foraging and perching, with usually one or two perched while the rest foraged. Third, a dominant male remained on watch and appeared to forage less than all the others.

DISCUSSION

Foraging time and flock size

Data suggest that there is a correlation between an increased flock size and increased male foraging time. While the trend was not significant when all data points were included (Fig. 2a), a positive trend was clearly present, and the removal of one data point caused the correlation to be significant (Fig. 2b). This positive relationship suggests that at least for males, flocking behavior has a beneficial effect on foraging by increasing foraging time.

Since males were the ones who dominated the role of scanning, an increased number of males to the group may have increased the amount of time each one was able to feed. On the other hand, the increase in number of males may simply be an artifact of increasing group size: more males meant nothing more than larger flock size and the increase of males did not play a direct role in the increase of foraging time.

I hypothesized that an increase in flock size would not significantly increase the number of antagonistic interactions among males or have a significant effect on foraging time. It turned out that antagonistic interactions had no effect on foraging time since none were ever observed among *T. olivacea* individuals during the course of this study.

Instead males may have interacted via calling; calling in wrens is known to function as predator avoidance and as territory defense (Morton and Shalter 1977). Lack of hostile interactions surely played a role in allowing males to feed more instead of fight. Reasons for this absence of hostility are unknown but possibilities are inherence in *T. olivacea* behavior, or the lack of competition for food resources.

Explaining the data

It is difficult to explain the lack of significance in the data when including all data points. It is unknown whether foraging patterns observed in the flock of 50 individuals reflect typical flocks of this size since no other groups of this size were observed.

The weakness of the correlation between flock size and foraging time when considering all data may have been a result of reduced predation. As no predatory birds were observed during this study or in a concurrent bird survey conducted in the same area (Kovacs 2004), it may be possible that *T. olivacea* individuals in the San Luis valley area are not threatened by predators and do not need to scan for predators as much. It has been suggested that birds that are less vulnerable to predation show less of a correlation between time spent scanning and flock size (Sparling and Krapu 1994).

Another possible explanation for the weak positive correlation is that the relationship between foraging time and flock size levels off and asymptotes. This means that there is a cap to time for foraging and any increase in flock size thereafter will have no increase in foraging time. Flocking can only do so much because a bird still must spend its time elsewhere such as perching to rest or calling for communication.

A recent study speculated that birds at colder temperatures spent more time moving to increase their body temperature, and less time calling to save energy, while birds at warmer temperatures did the opposite (Godfrey and Bryant 2000). In this study, the majority of a male's time was spent perching, scanning, or calling. It may be possible that because the majority of days were sunny and hot, *T. olivacea* individuals were trying to compensate for the excess heat through reduced movement and repeated calling.

Why not always flock?

Flocking, in this study and others, has been show to be beneficial to birds as it allows more time to forage. Yet numerous birds were observed in small flock sizes or not in flocks at all. A logical conclusion is that, in spite of the benefits of flocking, birds find it more beneficial, or at least not less beneficial to not flock.

Birds may simply not need to feed at the increased foraging time offered in flocks. As grass seeds are abundant in the San Luis Valley area and temperatures remained relatively moderate during this study, *T. olivacea* individuals were probably never drained of energy reserves and would not need to maximize their foraging time. In fact, two of the individual males observed were more plump than any other males or females seen in flocks, suggesting that they were well-fed even though their observed forging times were not high. If flocking benefits are not of any great assistance to birds, than there should be no reason to expect more to flock than to not flock.

The possible lack of small-bird predators in San Luis may make flocking for protection and predator-defense purposes less necessary. It is more likely that birds

would be seen outside of flocks or in smaller flocks when their survivorship is not negatively affected by doing so (Krebs and Davies 1981).

While this study showed flocking is beneficial to foraging time and does not have costs in terms of antagonistic interactions (i.e. none were seen), there are many other factors that contribute to a bird's choice to flock. Other costs of flocking include conspicuousness and other benefits include territory defense (Krebs and Davies 1981). One important benefit outweighing those of flocking pertains to mating. It makes sense that males in smaller flocks (especially male/female pairs) may have more access to females. Males may sacrifice increased foraging time offered by a flock for a mate. Males in all four male/female pairs in this study, remained perched while females foraged, plausibly giving up their foraging time, and scanning for predators so the female wouldn't have to. Sacrificing foraging time (time which may be unnecessary anyway) for to keep a mate may outweigh benefits of foraging provided by flocking. Moreover, finding a new mate is a cost for a bird, and because a female incurs this cost to a greater extent when in a pair than when in a flock with many nearby males, she may be less likely to leave her partner (Dhondt and Adriaensen 1994).

Conclusions and future studies

This study primarily reports on patterns and behavior observed in males of *T. olivacea*. Future studies might examine foraging behavior and other patterns in *T. olivacea* females in different group sizes. Other interesting studies might focus on locations where pastureland and grassy plants are a limited resource and see how foraging behavior of *T. olivacea* individuals differs. Additionally, quantitative studies to follow up qualitative data reported in this study are needed, such as precise amounts of time spent calling or scanning, and support for *T. olivacea* occurring in mixed-foraging flocks. Finally, more studies on gains and losses of flocking behavior are needed for tropical bird species which would be useful in comparison to observed patterns in temperate species.

ACKNOWLEDGEMENTS

I would like to thank my mother, Jennifer Blair, for always supporting everything I do, no matter how crazy it may be. Thanks to both Alan, my primary advisor, and Karen Masters, too, for your help with the project and for your dedication to tropical conservation. Thanks Matt Gasner for getting me started with Yellow-faced Grassquits. Thanks to Javier Mendez for your help with the "resumen" and to Ollie Hymen for your help with the paper. Thank you Joanna Hsu for butterflying while I bird watched. Thank you Nori for your help in the field (even though we didn't see any birds that day).

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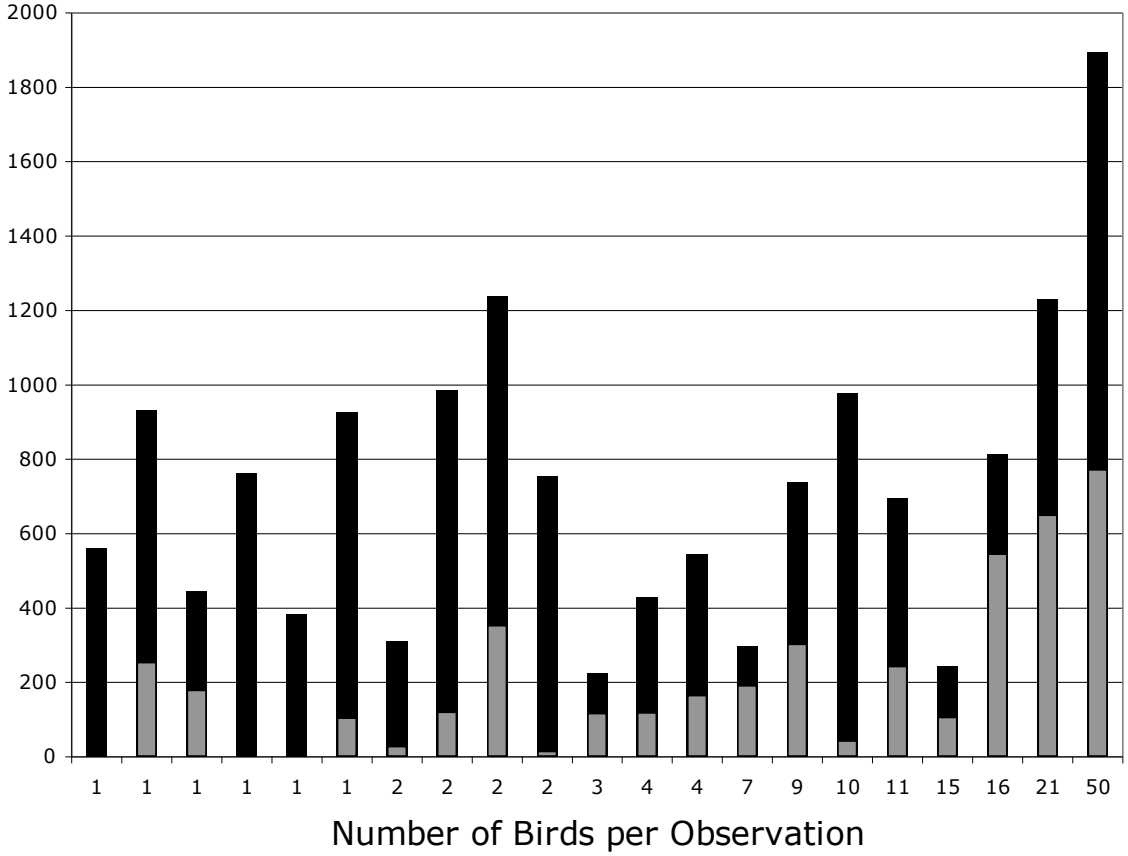


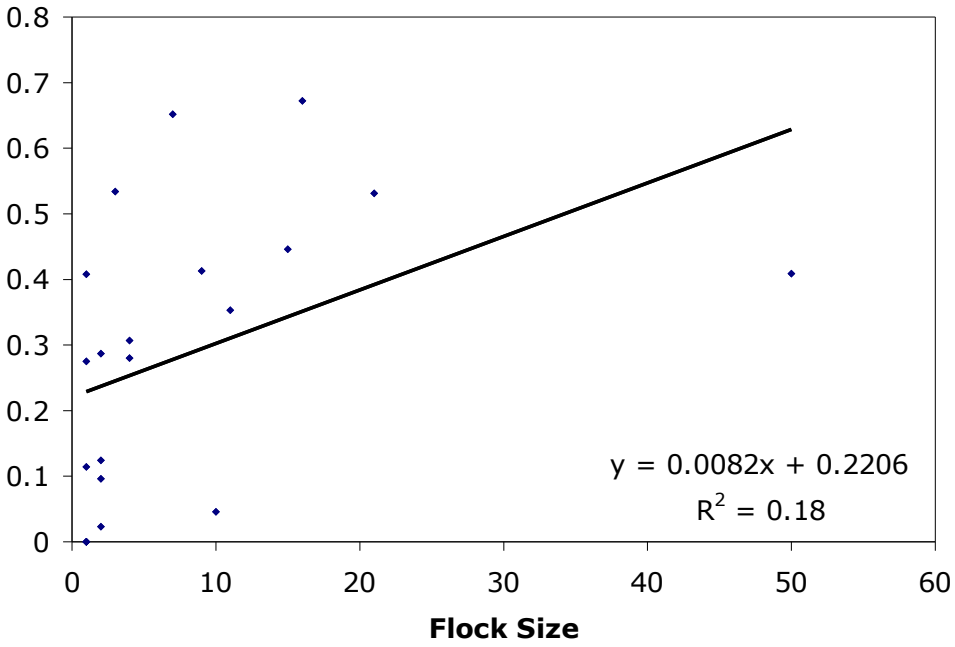
Figure 1. A total of 21 observations of *T. olivacea* were made. Observation times ranged from a maximum 31 minutes 34 minutes to a minimum of 3 minutes 43 seconds, with an average observation time of 12 minutes 18 seconds (± 6 min 41 sec). Time spent foraging (grey) and non-foraging (black) were also recorded for an individual male within the group.

Table 2. Flock size and sex composition for 21 observations of *T. olivacea*.

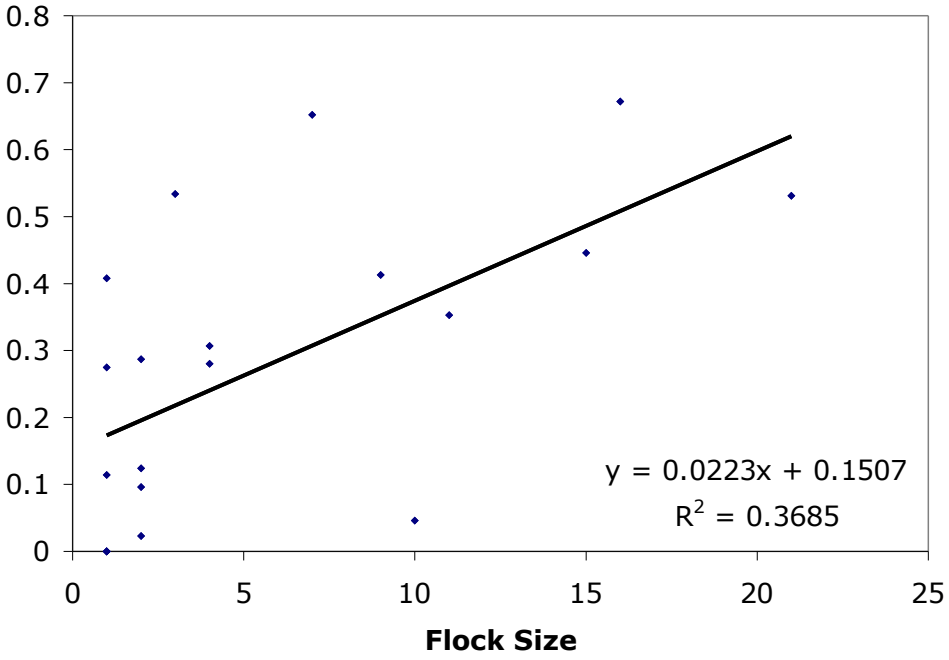
Number of Birds (flock size)	Number Males (M): Number Females (F)
1	1M
1	1M
1	1M
1	1M
1	1M
1	1M
2	1M:1F
2	1M:1F
2	1M:1F
2	1M:1F
3	1M:2F
4	2M:2F
4	3M:1F
7	5M:2F
9	3M:6F
10	6M:4F
11	6M:5F
15	6M:9F
16	6M:10F
21	13M:8F
50	22M:28F

Table 1. Sally times (min:sec) of male *T. olivacea* from two different flock sizes

	1 male		9 birds (3 males 6 females)	
	foraging	non-foraging	foraging	non-foraging
sally 1	00:51	11:51	00:30	00:45
sally 2	00:50	00:29	01:47	02:12
sally 3	00:05	01:20	00:44	00:20

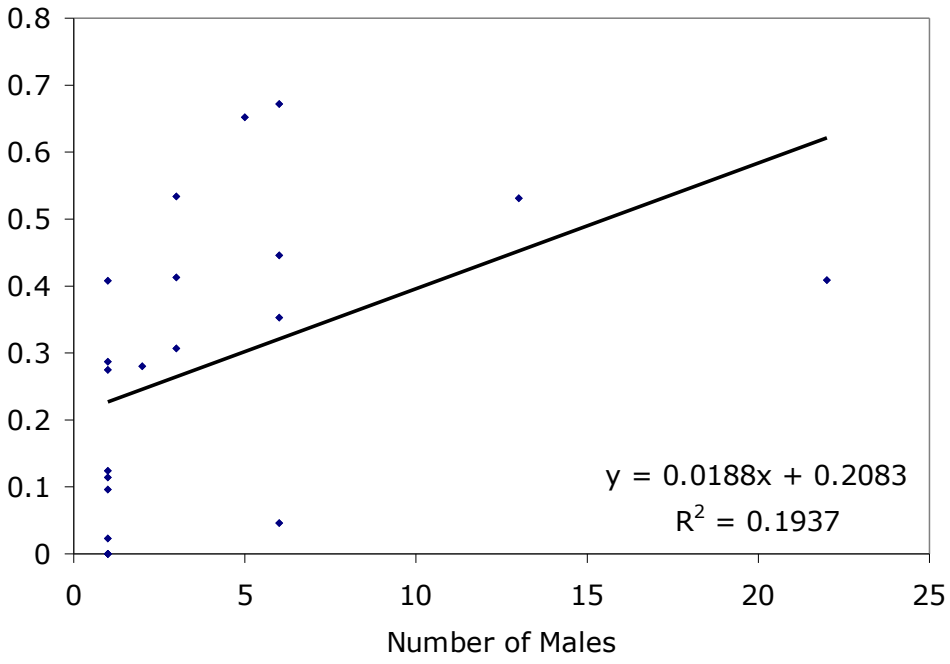


a)

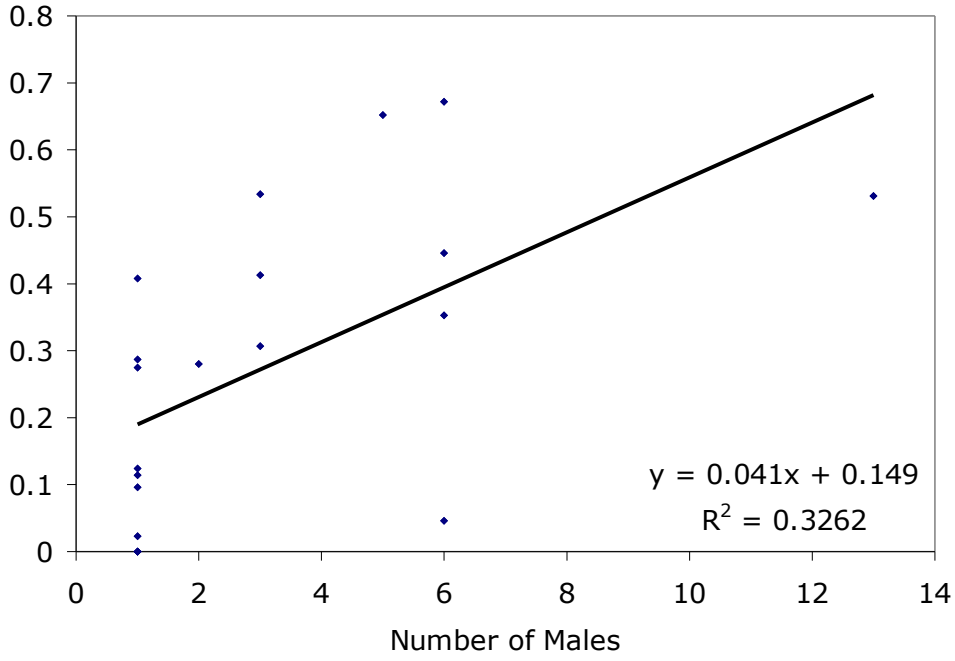


b)

Figure 2. Positive trend was found between group size of *T. olivacea* and percent of time spent feeding, but the correlation was not significant ($p = 0.0553$, $R^2 = 0.18$, $n = 21$) (a). Data point (group size = 50) appeared to be an outlier, and when it was removed from the data set, a significant correlation was found ($p = 0.0045$, $R^2 = 0.3685$) (b).



a)



b)

Figure 3. There is a positive trend between the number of *T. olivacea* males foraging together and the percentage of time each individual spends actually foraging (a), however, this correlations is not significant ($p = 0.0707$, $R^2 = 0.1617$) unless an outlier data point (group size = 50, $p = 0.0227$, $R^2 = 0.2563$) is excluded (b). Correlation may because an artifact of an increase in males also is an increase in flock size.

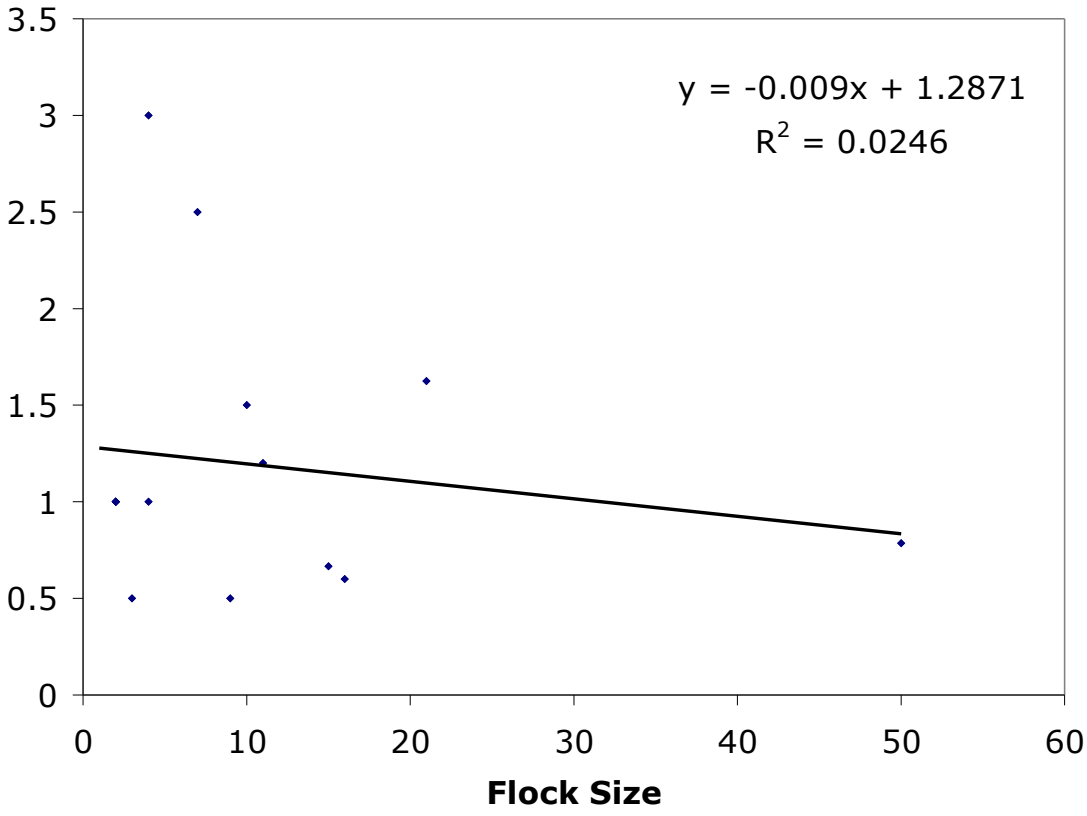


Figure 4. In 15 populations of *T. olivacea* (6 solitary male *T. olivacea* observed are not included) no significant correlation was found between the group size and sex ratio with ($p = 0.8124$, $R^2 = 0.0246$) or without the outlier point ($p = 0.8889$, $R^2 = 0.0017$). This indicates that sex ratio in number of *T. olivacea* flocks independent of flock size.

Reasons behind flocking differ among birds, but include nesting, courtship, predation, and foraging. Birds may come together for the mutualistic benefit of nest defense, although this hypothesis has been challenged by recent studies (Olendorf 2004). Males of a species may temporarily flock to form leks during the mating season to attract females and enhance courtship displays (Foster 1985). I hypothesized that in smaller groups, males would have higher foraging gains, because while they would have to dedicate more of its own time to scanning for predators, they would engage in fewer antagonistic interactions with other males and females.

It makes sense that the primary habitat of *T. olivacea* is weedy fields, pastures, and roadsides and primarily feed on grass seeds only eating insects or berries when seeds are rare Their primary habitat is, and they

Possible reasons for the outlier point include lack of data at similar group sizes and foraging gains asymptote at a certain group size.

Birds are the most endothermic of animals (some over 41 degrees) and often die of overheating (Longrich 1997). Therefore, it is logical that many of the birds would spend the majority of their time perching and calling, and remain sheltered on exceptionally hot days.

Furthermore, time spent watching for predators does not always show a direct correlation with group size (Sparling and Krapu 1994).

or may be a result of the study being conducted during the non-breeding season (Stiles and Skutch 1989). Territorial aggression in highest in the non-breeding season for wrens (Morton and Shalter 1977), but

Changes in flock size affect the foraging patterns of individuals within a group. In itself, flocking may either decrease or increase foraging time of a bird. It has been noted that both) show an increase in antagonistic interactions as flock size increases. On the other hand, an increase in flock size can also increase foraging time of birds. Flocking interactions allows some birds to remember locations of food patches as well as detect good and bad changes in foraging gains discovered by another bird's sampling (Krebs and Inman 1994). combined with the effects of predation In a study of rooks, birds were shown to alter their foraging behavior in different flock sizes to maximize their energy gain from the food: members of smaller groups feed on larger food items and have to spend less time feeding, but birds in larger groups, although they eat smaller prey items, dedicate more time to feeding and consume food at a faster rate (Hart 1991). Here

Perhaps the most important connection between predation and foraging in bird flocks is that an increase inIn many bird species there is a correlation between predator defense and foraging.

Larger flocks can both Flocks sizes have been reported to have various affects on the foraging and feeding gains of birds. Some studies have shown no change in foraging gains with a change in flock size: Flocking may even negatively affect foraging, as an increase in population increases This, in turn, may While some birds in a flock are less successful than others at foraging, most birds appear to benefit from flocking behavior (Rowcliffe 2004). Flocking behavior is probably most often beneficial, as the trait is genetically maintained by many bird species (Beauchamp 2004). Group interactions Flocking behavior may also contribute to foraging gain of birds indirectly. Flock size can reduce predation by increasing the number of birds that scan and survey for predators (Powell 1985).

While *T. olivacea* is known to eat berries and insects as well as grass seeds, the two former resources are eaten only when grass seeds are rare (Stiles and Skutch 1989). It is highly unlikely that grass seeds were a limited or limiting resource because of the numerous pastures and fields in the San Luis Valley. Moreover, as individuals of *T. olivacea* individuals were observed eating only grass seeds, it is highly unlikely grass seeds were a limited resource. Their diet may explain why *T. olivacea* were only sited and observed in grassy open areas and never in forests.

The sex ratio in *T. olivacea* populations had no significant correlation to flock size. Sex ratios tend to be skewed primarily when investment in different sexes differs, and usually the sex requiring less investment will be produced in greater numbers (Ricklefs 1990). No trend in sex ratio perhaps suggests no changes in stresses in terms of predation, food resources, or environmental conditions as group size increased.

Male ducks, for example often take dominant foraging spots or exclude females from prime foraging habitat (Alexander 1987). However, male generosity shown to females is possible, too: one study on Double-crested Cormorants shows that males fly farther to forage, leaving closer, more plentiful areas to females (Anderson et al. 2004).

The birds, however would stay within a certain distance from a central tree or tree line. When a bird would occasionally get startled (e.g. by a vulture flying overhead), it would fly back to the tree central tree, and all the other birds would follow. The birds would call while they flew back to their perches.

The microhabitats in which *T. olivacea* were observed in this study are similar to the habitats in which they are typically found (Stiles and Skutch 1989). The two preferred microhabitats were those with one or more trees, probably selected because they offered more shade and protection against predation (Cuadrado 1997) than did a completely open, grassy microhabitat.

Of the six solitary males observed, the one that was observed foraging for the longest period of time foraged in proximity to two Golden-bellied Flycatchers (*Myiodynastes luteiventris*).

while the rest in the flock would forage. After a few minutes, a foraging bird would return to its perch, relieving a perched bird that would then fly down and begin foraging. Usually at least one male remained perched, but occasionally a scanner was a single female.

It seems possible that the individual *T. olivacea* male seen foraging in proximity to the Golden-bellied Flycatchers did comprise a mixed foraging flock. *Tiaris olivacea* is a species known to group with other seedeaters (Stiles and Skutch 1989), and while Golden-bellied Flycatchers are insectivores, not seedeaters (Stiles and Skutch 1989), mixed foraging flocks of species with different foraging niches are also common (Chen and Hsieh 2002). A mixed-foraging flock would confer the same advantages as a *T. olivacea* flock allowing the male to spend more time foraging (Chen and Hsieh 2002), which could explain why this male had a higher percent of time feeding than the other solitary males.

The three males of the non-flocking group of *T. olivacea* never directly interacted, although their consecutive calling may have been a form of territory marking or a spacing mechanism. In wrens, calling functions as predator avoidance and as territory defense (Morton and Shalter 1977). Perhaps the lone males of *T. olivacea* were calling to define their territory to the other nearby males.

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