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LES EFFETS DE PLUSIEURS TYPES DE PROIES DANS UN JEU PRODUCTEUR-CHAPARDEUR DÉPENDENT DE LA CRYPTICITÉ CHEZ LE CAPUCIN DAMIER (*Lonchura punctulata*)

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THE EFFECTS OF MULTIPLE PREY TYPES IN A PRODUCER-SCROUNGER GAME DEPEND ON PREY CRYPTICITY IN NUTMEG MANNIKINS (*Lonchura punctulata*)

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RÉSUMÉ

La crypticité est une stratégie employée par divers organismes afin d'éviter d'être détectés par leurs prédateurs. Lorsqu'un prédateur solitaire doit rechercher plusieurs types de proies cryptiques simultanément, cette recherche devient plus difficile qu'en présence d'un seul type. Le prédateur subit ainsi une diminution de la précision et de la vitesse d'alimentation. Cette diminution est due au phénomène d'attention limitée: la capacité mentale des animaux ne permet de traiter qu'une certaine quantité d'information à la fois. En divisant son attention entre les différentes proies disponibles, le prédateur devient moins efficace à retrouver toutes ces proies. Les effets de la crypticité des proies sur les prédateurs sociaux ont rarement été étudiés, et la recherche de plusieurs types de proies cryptiques n'a jamais été examinée dans un contexte d'approvisionnement en groupe. Chez les prédateurs grégaires, l'alimentation peut prendre la forme d'un jeu producteur-chapardeur, où chaque membre d'un groupe peut alterner entre deux tactiques d'approvisionnement mutuellement incompatibles: rechercher activement ses proies (tactique producteur), ou se joindre aux découvertes des autres (tactique chapardeur). La proportion de chapardage dans un groupe devrait augmenter lorsque les coûts associés à la tactique producteur augmentent. Bien que les effets négatifs d'une diminution de la vitesse d'alimentation en présence de proies cryptiques soient sentis également par les producteurs et les chapardeurs, les coûts énergétiques et temporels associés à une augmentation de la fréquence des erreurs de détection sont connus exclusivement par les producteurs. La présence d'une proie cryptique devrait donc mener à un accroissement de la proportion du groupe qui s'adonne à la tactique chapardeur, avec une plus grande augmentation lorsque plusieurs types de proies cryptiques sont disponibles. Pour vérifier cette prédiction, des groupes de Capucins damiers (*Lonchura punctulata*) ont recherché un ou deux types de proies (graines rouges et jaunes) sur deux substrats sur lesquels les graines apparaissaient visibles ou cryptiques. Nos résultats confirment que la crypticité des proies entraîne une diminution de l'efficacité d'alimentation des prédateurs sociaux puisque les oiseaux font plus d'erreurs de détection et s'alimentent moins rapidement lorsque les proies sont cryptiques que lorsqu'elles sont visibles. La présence simultanée de plusieurs types de proies cryptiques intensifie également ces effets négatifs, réduisant davantage l'efficacité d'alimentation. La proportion de chapardage dans le groupe augmente de la condition visible à la condition cryptique, ainsi que lorsque deux types de proies cryptiques sont disponibles relativement à un type de proie cryptique. Cependant, les oiseaux diminuent le comportement de chapardage dans la condition visible lorsque plusieurs types de proies sont présents, un résultat que nous ne pouvons pas expliquer avec cette étude. Nos résultats suggèrent que la crypticité serait une stratégie anti-prédatrice plus efficace contre les prédateurs sociaux que les prédateurs solitaires, et que le polymorphisme chez les espèces proies cryptiques a évolué en partie pour diminuer la pression de prédation provenant des animaux sociaux.

Mots-clés: approvisionnement social, producteur-chapardeur, proie cryptique, polymorphisme, Capucin damier.

ABSTRACT

Crypsis is a strategy employed by numerous prey species in order to avoid detection by visual predators. For a solitary predator, searching for multiple cryptic prey types simultaneously reduces foraging efficiency relative to searching for a single cryptic prey type: the predator experiences slower feeding rates and reduced accuracy of detection. This reduction in foraging efficiency is due to limited attention, as animals can only process a limited quantity of information at any given time. By dividing its attention between different cryptic prey types, the predator becomes less efficient at detecting all available types. While the effects of cryptic prey on solitary predators are well documented, few studies have examined prey crypticity in a social foraging context, and none have examined the effects of multiple cryptic prey types on group foragers. For social predators, each individual in a group can alternate between two mutually exclusive foraging tactics: actively searching for food, the producer tactic, or searching for opportunities to join the food discoveries of others, the scrounger tactic. The pay-offs to each tactic will affect their relative use within the group, and so when the costs associated with the producer tactic increase, the proportion of scrounger use should also increase. The lower feeding rates encountered when foraging for cryptic prey will be felt equally by individuals engaged in both tactics. However, the time and energy costs associated with more frequent detection errors while searching for patches of cryptic prey are exclusive to those individuals engaged in the producer tactic. The presence of cryptic prey should thus increase scrounger use in a group, and searching for multiple cryptic prey types simultaneously should even further increase use of this tactic, as the costs to producing increase due to more frequent detection errors. In order to test this prediction, groups of nutmeg mannikins (*Lonchura punctulata*) searched for one or two prey types (red and yellow millet seeds) on two foraging substrates on which the prey appeared cryptic or conspicuous. Birds make more frequent detection errors and feed at slower rates when prey are cryptic than when conspicuous, confirming that cryptic prey reduces foraging efficiency in social predators. A further decrease in foraging efficiency is observed when two cryptic prey types are present. In addition, groups increase their use of the scrounger foraging tactic when prey are cryptic, with a small further increase in scrounging when two cryptic prey types are available. Unexpectedly, birds scrounge less when two conspicuous prey types are present relative to one conspicuous prey type. These results suggest that crypsis may be a more effective anti-predator strategy against social predators than against solitary predators, and that cryptic prey polymorphism may have evolved partially in response to differences in social predator foraging tactic use.

Key words: social foraging, producer-scrounger, cryptic prey, polymorphism, nutmeg mannikin.

GENERAL INTRODUCTION

Predator-prey interactions and crypsis

There exists an arms race between predator and prey species: as predators become better at capturing their prey, so do prey become better at avoiding being captured. On evolutionary time scales, this leads to increasingly more efficient counter-adaptations between predators and prey (Dawkins & Krebs 1979). Encounters between predators and their prey usually adhere to the following progression: detection, identification, subjugation, consumption (Endler 1986). Interrupting this sequence is essential for a prey's survival, and one way of accomplishing this is through its physical appearance. Prey that are cryptic, that closely resemble the background on which they appear, may go unnoticed by predators, reducing the likelihood of detection. Prey can also mimic a non-edible object, like a leaf or a branch, eluding correct identification. Conspicuous aposematic coloration can indicate to the predator that a particular prey item possesses chemical defenses employed in the subjugation and consumption stages, thus leading to its avoidance (Endler 1981, 1988). While disrupting the sequence at any of the four stages can lead to the survival of the prey, an interruption at one of the earlier stages is most advantageous, allowing it to conserve its energy for future predator encounters (Endler 1991). Hence, crypsis is an efficient and widely dispersed anti-predator adaptation, allowing prey to escape predator attack by altogether avoiding detection (Endler 1978).

A prey that is cryptic resembles a random sample of the background as it is perceived by the predator, at the age, time and in the microhabitat for which the prey is most susceptible to predation (Endler 1978). For instance, Endler (1984) noted that moth species assemblages in a northern temperate forest change over the course of the seasons, with different species' adult forms emerging at different times. The adults best match the forest background found at the time of their emergence, and some species are highly selective of the substrates on which they rest in order to maximize crypticity. Thus, the moths are cryptic in their adult forms at their usual times of emergence, and in certain cases on the substrates for which they are specialized; at a different time, age or background, these moths would not be cryptic to their predators. Prey possessing cryptic coloration undoubtedly experience lower predation rates than more visible prey. For example, marine snails (*Littorina saxatilis*) with cryptic shell colors have greater survival than those with conspicuous shells when predated upon by visual predators (Johannesson & Ekendahl 2002). Likewise, in three species of juvenile flatfish (English sole *Parophrys vetulus*, northern rock sole *Lepidopsetta polyxystra* and Pacific halibut *Hippoglossu stenolepis*), individuals that match the background are less vulnerable to predation by adult halibut than those that contrast with the background (Ryer et al. 2008).

Cryptic prey and solitary predators

Effects on foraging efficiency

The effects of prey crypsis on the foraging efficiency of solitary predators have been greatly explored. When prey are cryptic, predators are slower to detect their presence, both to initiate foraging and during searching. This leads to longer detection times, as well as lower search speeds and feeding rates (Dawkins 1971a, Bond 1983, Lawrence 1985a,b, Gendron 1986, Bond & Kamil 1999, Johnsson & Kjällman-Eriksson 2008). In addition, because cryptic prey so closely resemble the substrate, predators can confuse parts of the background for the prey itself and attempt an erroneous capture (Dawkins 1971a, Bond 1983, Bond & Kamil 1999, Dukas & Kamil 2000). These detection errors can be costly in terms of both time and energy. Foraging efficiency can be even further decreased when cryptic prey appear on a more complex background consisting of many contrasting elements, which requires a longer and more thorough search in order to locate prey (Merilaita 2003, Bond & Kamil 2006). Predators may however improve their ability to detect and capture cryptic prey by forming a search image.

Search images

Luuk Tinbergen (1960) first used the term "search image" to describe the selective foraging on cryptic prey by great tits (*Parus major*), which tended to overselect the most frequent prey type occurring within their habitat. He suggested that repeated encounters with this prey type activated a perceptual bias that allowed the birds to improve their ability to detect the prey against the substrate. While use of the term has sometimes diverged from its original meaning (e.g. Nams 1997), search images generally refer to a predator's improved detection of a cryptic prey type through a mental representation of the prey, allowing it to be more easily distinguished from the background and thus improving detection and increasing search speed. There is some question as to whether this representation is of the prey stimulus as a whole, or rather selective attention to the specific features of the prey that allow it to be distinguished from its surroundings. Langley (1996) tested this directly, and found that by changing a particular aspect (color or shape) of a prey item that pigeons had been searching for, the birds showed reduced accuracy and speed. These results suggest that the search image the birds had formed was no longer effective, and that foragers tune in to specific elements of a prey item when forming a search image.

A forager's efficiency to feed on cryptic prey improves with repeated encounters with the same prey item. Individuals typically improve their detection ability and increase their search speed as they become more experienced with a particular cryptic prey type, suggesting that a search image is reinforced with successive captures of the same item (Pietrewicz & Kamil 1979, Lawrence 1985a,b, Gendron 1986, Plaisted & Mackintosh 1995, Langley et al. 1996). Indeed, predators often feed selectively in runs of the same cryptic prey type, and show a bias towards the particular cryptic prey they have had previous experience with when given a choice of food items (Dawkins 1971b, Reid & Shettleworth 1992, Langley 1996).

Limited attention

This bias towards previously-experienced prey indicates that searching for cryptic prey involves constraints related to limited attention. An animal's mental capacity is limited to processing only certain amounts of information at a time, and the more abundant and complex the information, the less likely an animal will be able to process it all (Dukas 2002). If tasks become more difficult or if numerous different tasks are undertaken simultaneously thus dividing attention, then performance will be negatively affected. Research on humans and monkeys in the fields of psychology and neurobiology has shown that focusing attention on specific tasks activates and enhances the response of the neurons processing the stimuli involved, all the while suppressing activity in the neurons that process other stimuli (Dukas 2002, 2004). For example, Dukas & Kamil (2000) found that blue jays (*Cyanocitta critata*) trained to search for digital caterpillar images are less likely to detect a peripheral moth target when the caterpillars are made more cryptic against the background. Stated otherwise, when attention is focused on the more complex digital caterpillar stimuli, birds are less able to process the peripheral target stimuli. The authors liken this peripheral target to an approaching predator, and thus conclude that limited attention would limit a bird's ability to detect predators when the foraging task is cognitively engaging. Similarly, Griffiths et al. (2004) showed that for territorial species, associating with familiar conspecifics allows individuals to focus more attention on feeding and predator vigilance by reducing the need to allocate attention to aggression: juvenile brown trout (*Salmo trutta*) in familiar groups respond faster to the presence of a predator, feed at higher rates and have fewer aggressive interactions than those in unfamiliar groups. As such, fish in unfamiliar groups that need to allocate part of their limited attention to aggression are less efficient at other tasks, namely foraging and predator detection.

However, when a task is simple and requires less attention, limited attention no longer becomes an important constraint on performance. For instance, Dukas & Ellner (1993) constructed a model in order to predict the number of prey types a predator should pursue, and how to divide attention between them. They found that when prey are equally conspicuous and are also equal in abundance and reward, a forager would obtain maximum energetic benefits by searching for and consuming all prey types. Conversely, when a predator encounters multiple equally cryptic prey types that differ in appearance but are equal in abundance and reward, the optimal diet consists of focusing on a single one of those prey types. Therefore, in the case of foraging for cryptic prey, focusing attention on a single type seems to be the best option, while for conspicuous prey, attentional limitations no longer demand a specialized search. The constraints of limited attention require foragers to carefully allocate their attentional resources in order to balance all their needs, most notably obtaining food and avoiding predation (Clark & Dukas 2003).

Multiple cryptic prey types

Limited attention restricts the ability of predators to search for cryptic prey when multiple different types are available, as they seem only to be capable of efficiently searching for one cryptic prey type at a given time. Numerous experiments have shown that dividing attention by foraging on multiple cryptic prey types at once or switching from one prey type to another leads to costs, such as slower detection times and more frequent detection errors (Pietrewicz & Kamil 1979, Plaisted & Mackintosh 1995, Langley 1996, Dukas & Kamil 2001). In terms of search images, this implies that they cannot be formed for multiple prey types simultaneously, and that foraging on an alternative prey type interferes with a previously formed search image and prevents it from being maintained (Plaisted & Mackintosh 1995). When multiple cryptic prey types are available, foragers must therefore choose between dividing their attention amongst all the types and becoming less efficient or focusing attention on one prey type in order to maximize performance. It is however possible that foragers are unable to focus attention on one cryptic prey type by forming a search image when the different types are equally abundant in the environment. A search image is defined as an increase in detection ability through repeated capture of the most common prey type (Tinbergen 1960), and there is some experimental evidence that search images will in fact only be formed when one prey type is in the majority (Bond 1983). Only by repeated chance findings of the most common cryptic prey type will the predator develop a perceptual bias for it, which then causes it to overselect this prey relative to its actual abundance in the environment. Regardless of whether predators are actually capable of specializing when prey types are equal in abundance, there is substantial empirical support that they do indeed overselect the prey type that is in the majority and that repeated capture of the same prey leads to enhanced performance (Bond 1983, Gendron 1986, Bond & Riley 1991, Reid & Shettleworth 1992, Langley 1996, Bond & Kamil 1999).

Apostatic selection and prey polymorphism

This negative frequency-dependent selection of predators favoring the survival of rare cryptic prey over more common cryptic prey is also referred to as apostatic selection. As predators focus attention and become more efficient at capturing common prey types, rarer alternatives are overlooked. For polymorphic prey species with many different existing phenotypes, predators will effectively ignore rarer morphs, which should support the development of new morphs and stabilize existing ones (Allen 1988, Bond 2007). To verify this, Bond & Kamil (2002) had blue jays search for various digital moth morphs on backgrounds on which they appeared cryptic. The moths evolved according to a genetic algorithm, with those that were not detected or slower to be detected by blue jays more likely to breed. They found that moths became progressively more cryptic and variable than control moth lineages, as blue jays overlooked the atypical, more cryptic moths. In the field, Olendorf et al. (2006) manipulated the ratios of male guppy (*Poecilia reticulata*) color morphs by transferring individuals between different pools in order to create populations with various morph ratios. They found that rare morphs had greater survival than common ones, and suggest that predators form search images for common morphs and are better able to detect them. Thus, both laboratory and field studies show support for the maintenance of prey polymorphisms via apostatic selection in favor of rare cryptic morphs. Polymorphism is indeed common in cryptic prey species and is especially widespread in insects, although it has also been recorded in mollusks, crustaceans and vertebrates (Bond 2007).

Cryptic prey and social predators

Effects on foraging efficiency

Relatively few studies have examined the effects of foraging for cryptic prey on social predators, and none have looked at the effects of the presence of multiple cryptic prey types. It remains unclear whether social predators respond as solitary predators do, but the available evidence suggests that searching for cryptic prey is more difficult for the former than for the latter. Courant & Giraldeau (2008) studied nutmeg mannikins (*Lonchura punctulata*) foraging for cryptic or conspicuous white millet seeds in the presence or absence of a conspecific. They found that birds eat fewer seeds and peck less accurately when foraging with a conspecific than when feeding alone, but only when seeds are cryptic; there is no effect of conspecific presence on feeding efficiency when the seeds are conspicuous. Furthermore, they found that these negative effects of group foraging on cryptic seeds persist even when the conspecific is subsequently removed from the foraging area, as birds that have previously fed on cryptic seeds in the presence of another bird eat fewer seeds and are less accurate than birds that have only ever foraged alone. The authors suggest that self-imposed interference effects lead to reduced feeding efficiency on cryptic prey in the presence of another individual, and that the monitoring of a conspecific limits the attention available to acquire and develop a search image.

Producer-scrounger game

Courant & Giraldeau's (2008) study, which used a dispersed rather than clumped distribution of seeds, did not look at an additional aspect of social foraging. When food is clumped and can be shared between group members, individuals can join the food discoveries of others, thus benefiting from additional feeding opportunities beyond what they discover for themselves. If this phenomenon conforms to an information-sharing model, a forager is capable of simultaneously searching for food and monitoring flock members in order to join in their discoveries; accordingly, an individual incurs no costs by both finding and joining feeding opportunities, and will join whenever the occasion arises (Giraldeau & Beauchamp 1999). However, when the tactics are mutually exclusive, when looking for joining prospects precludes searching for one's own food and vice versa, this type of group foraging conforms to a producer-scrounger (PS) game, where individuals playing producer search for food, and those playing scrounger search for producers that have found food in order to join them (Barnard & Sibly 1981).

The pay-offs to the producer and scrounger tactics are frequency-dependent, determined by the proportion of scroungers present in a group. When scrounging is rare, scroungers generally do better than producers as there are a greater number of discovered food patches for them to exploit, with a small number of scroungers that will share each patch. When scrounging is common, scroungers do worse than producers because there are fewer food patches discovered, each of which must be competed for by the more numerous scroungers (Barnard & Sibly 1981). This frequency-dependence leads to the eventual formation of a stable equilibrium frequency (SEF) of scrounger use in a group, where the pay-offs to both tactics are equal. Mottley & Giraldeau (2000) have shown experimentally that flocks of nutmeg mannikins do indeed conform to a predicted SEF of scrounger when engaged in a PS game. Individuals foraging in a PS game can make exclusive use of one tactic, or as is more often observed, they can alternate between the two tactics (Giraldeau et al. 1990, Giraldeau et al. 1994, Koops & Giraldeau 1996, Beauchamp 2001). The PS game has been demonstrated in many species of ground-feeding birds, including zebra finches (*Taeniopygia guttata*) (Giraldeau et al. 1990, Beauchamp 2001, Beauchamp 2006), nutmeg mannikins (Giraldeau et al. 1994, Coolen et al. 2001, Wu & Giraldeau 2005), starlings (*Sturnus vulgaris*) (Koops & Giraldeau 1996), house sparrows (*Passer domesticus*) (Barnard & Sibly 1981, Liker & Barta 2002), northwestern crows (*Corvus caurinus*) (Ha & Ha 2003), Carib grackles (*Quiscalus lugubris*) (Morand-Ferron et al. 2007) and pigeons (*Columba livia*) (Giraldeau & Lefebvre 1986).

The PS game has been developed as a rate-maximizing model, in which individual decisions on tactic use are based on the maximization of food intake rate (Vickery et al.

1991). Alternatively, Caraco & Giraldeau (1991) developed a risk-sensitive model, in which foragers engage in either tactic based on the minimization of starvation risk. This latter model is built on the assumption that scrounging is a risk-averse tactic, while producing is a risk-prone tactic: variability in food intake is lesser when foraging as a scrounger. A number of empirical studies have shown that scrounging is indeed a risk-averse tactic (Koops & Giraldeau 1996, Lendvai et al. 2004, Wu & Giraldeau 2005). Regardless of the differences between these two models, they both coincide in that the SEF of scrounger in a group is largely dependent on both the size of the group and the finder's share, the proportion of a food patch that is available exclusively to the producer that discovers the patch. Decreasing finder's share and increasing group size are both expected to increase the proportion of scrounging within a group (Vickery et al. 1991), and both have been shown experimentally (Coolen et al. 2001, Coolen 2002). Reducing the finder's share can in fact be considered equivalent to increasing the costs of producing, which leads to a decrease in producer tactic use. For example, nutmeg mannikins scrounge more when an energetic cost is imposed to producing by increasing the weight of lids that need to be flipped to access food (Giraldeau et al. 1994). Other factors that have been shown to affect the SEF of scrounger use in groups of social foragers include dominance status (Liker & Barta 2002), predation risk (Barta et al. 2004, Mathot & Giraldeau 2008), energetic state (Lendvai et al. 2004), as well as prey crypticity (Barrette & Giraldeau 2006).

Cryptic prey and the PS game

For groups of foragers engaged in a PS game, certain effects of foraging on cryptic prey will be felt equally by those engaged in the producer or scrounger tactics, whereas others will not. The costs of longer detection times and slower search speeds will be experienced by both producers and scroungers: while it is the producers' search that is slower, scroungers ultimately depend on them for their feeding opportunities. As such, all group members will have lower feeding rates when foraging on cryptic prey, regardless of the tactic they choose. However, the time and energy costs associated with more frequent detection errors when searching for patches of cryptic prey are exclusive to individuals engaged in the producer tactic. Only those group members that are actively looking for food will make patch-level detection errors, therefore not affecting those using the scrounger tactic. It is worth noting that although scroungers may make detection errors when feeding on cryptic prey located within a patch found by a producer, these errors at the level of individual prey items are also made by producers, and the associated costs are equal for individuals engaged in either tactic. Finally, the additional attention required to search for cryptic prey may divert attention from other demanding tasks such as predator vigilance (Dukas & Kamil 2000), which could add producer specific predation costs. These two producer exclusive costs, patch-level detection errors and divided attention, should lead groups to increase their SEF of scrounger when prey are cryptic.

Barrette & Giraldeau (2006) tested this with groups of nutmeg mannikins searching for white millet seeds made cryptic or conspicuous. If foraging for cryptic prey induces the aforementioned producer exclusive foraging costs, they expected to see an increase in the number of detection errors and a decrease in anti-predator vigilance, leading to higher scrounger use. They found that while birds make significantly more detection errors when prey are cryptic, there is no difference in the proportion of time allocated to anti-predator vigilance. The presence of cryptic prey thus imposes a producer specific time and energy cost in the form of more detection errors, but does not lead to reduced vigilance and a greater predation risk for producers. Nonetheless, there is a significant effect of prey crypticity on tactic use, as flocks of nutmeg mannikins increase their use of the scrounger tactic when seeds are cryptic.

If producer specific costs do indeed lead to an increase in scrounging when prey are cryptic, then greater costs should lead to a greater increase. By making a search task more challenging, producers may make more numerous detection errors, and a corresponding increase in scrounging should then be observed. Dividing attention between multiple cryptic prey types leads solitary predators to make more frequent detection errors (Dukas & Kamil 2001). Experimentally manipulating the number of prey types available and their crypticity thus makes an effective means of verifying the hypothesis that more frequent detection errors further increases scrounger use. Moreover, the effects of multiple cryptic prey types have never been tested on social foragers. As such it is not known if social predators will respond in a similar manner to solitary predators, with reduced foraging efficiency due to the effects of divided attention. Finally, because prey polymorphism is common in cryptic species (Bond 2007) and many cryptic prey species have overlapping distributions (e.g. moths, Endler 1984), the effect of multiple cryptic prey types on social foraging tactic use is highly ecologically relevant.

Objective and predictions

The broad purpose of this study is to examine how the number of prey types available and their crypticity affect the behavior of socially foraging predators. We used nutmeg mannikins, small granivorous passerines, as model predators and red and yellow millet seeds as model prey. We formed four flocks of birds, and each flock foraged for one and two types of millet seeds under both cryptic and conspicuous conditions. The crypticity of the seeds was adjusted by modifying the background on which they appeared. We measured both foraging efficiency (feeding rates, patch discovery rates, and number of detection errors) and the incidence of scrounger use in each group. We expect to record a reduction in foraging efficiency when prey are cryptic, and more so when two cryptic prey types are available relative to one cryptic prey type. We also expect to see an increase in scrounger use when prey are cryptic, with a further increase when two prey types are present due to the producer-specific costs of more frequent detection errors. Finally, we expect to see no change in tactic use from one to two conspicuous prey types, as attentional constraints are not an issue when prey are conspicuous and easy to detect.

THE EFFECTS OF MULTIPLE PREY TYPES IN A PRODUCER-SCROUNGER GAME DEPEND ON PREY CRYPTICITY IN NUTMEG MANNIKINS (*Lonchura punctulata*)

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S.S. and L.-.A.G. both participated in the development of ideas, hypotheses, predictions and methods presented in this study. S.S. was also responsible for experimentation (with the assistance of Kimberley J. Mathot), statistical analyses and writing of the article. L.-A.G. provided supervision and assistance during all phases of this study, as well as editing earlier drafts of the manuscript.

In order to limit the use of paper, literature cited in the following is presented in a common reference section at the end of the document.

ABSTRACT

Crypsis is a common anti-predator strategy employed by prey species, as it lowers the foraging efficiency of their visual predators. For solitary animals, many studies have shown that searching for multiple different cryptic prey types simultaneously is more challenging than searching for a single type, leading to a further reduction in foraging efficiency via lower feeding rates and more frequent detection errors. An animal's attention is limited to processing a certain quantity of information at a time; as such, a predator's performance is negatively affected by dividing its attention between many different cryptic prey types. The effects of prey crypticity on social predators have rarely been studied, and searching for multiple cryptic prey types has never been examined in a social foraging context. For social predators, each group member can alternate between actively searching for food (producer tactic) and searching for opportunities to join the food discoveries of others (scrounger tactic). The proportion of scrounger use in a group is affected by the relative costs of each tactic, and so individuals scrounge more when the producer tactic is more costly. While the negative effects of lower feeding rates when foraging for cryptic prey are felt equally by both producers and scroungers, the time and energy costs of more frequent detection errors are experienced exclusively by group members engaged in the producer tactic. The presence of cryptic prey should then lead to an increase of scrounger use in a group, with a further increase when multiple cryptic prey types are present due to more numerous detection errors. To verify this prediction, we tested groups of nutmeg mannikins (*Lonchura punctulata*) searching for one or two prey types (red and yellow millet seeds) made cryptic or conspicuous by modifying the background on which they appeared. Our results confirm that prey crypticity lowers the foraging efficiency of social predators, as birds have lower feeding rates and make more frequent detection errors when prey are cryptic than when conspicuous. This effect if amplified when foraging for two cryptic prey types, with birds experiencing a further reduction in foraging efficiency. Scrounger use in groups increases from the conspicuous to cryptic conditions, as well as when two cryptic prey types are present relative to when only one cryptic prey type is available. Birds however also scrounge less under conspicuous conditions when two prey types are present, which cannot be explained given our data. Our results suggest that crypsis may be a more effective anti-predator strategy against social predators than against solitary predators, and that polymorphism in cryptic prey species may have evolved in partial response to social predator foraging tactic use.

INTRODUCTION

Numerous prey species possess cryptic coloration in order to avoid detection by their visual predators. An organism is considered cryptic if it resembles a random sample of the background at the age, time and in the microhabitat for which it is most at risk of predation (Endler 1978). As such, a prey is not cryptic in itself: its visibility to predators is completely dependent on the background on which it is found. The temporal and spatial matching between a cryptic prey and its appropriate background undoubtedly confer anti-predator advantages through reduced predation (Johannesson & Ekendahl 2002, Ryer et al. 2008). Searching for cryptic prey is certainly challenging for solitary predators: they experience longer detection times, lower search speeds and feeding rates, and more frequent detection errors (Bond 1983, Lawrence 1985a,b, Gendron 1986, Bond & Kamil 1999, Johnsson & Kjällman-Eriksson 2008). In addition, the cognitively demanding task of looking for cryptic prey detracts attention from other tasks requiring attention, such as predator vigilance (Dukas & Kamil 2000).

When multiple cryptic prey types are present simultaneously, the above effects on solitary predators can be even more pronounced (Pietrewicz & Kamil 1979, Dukas & Kamil 2001). This is thought to be a consequence of limited attention because an animal's brain can only process certain amounts of information at a time (Dukas 2002). As a task becomes more cognitively difficult, or if an animal divides its attention among multiple concurrent tasks, performance is negatively affected. In humans and monkeys, performing particular tasks activates specific regions of the brain while suppressing others, and focusing on a task leads to enhanced neural activity of a region (Dukas 2002, 2004). Consequently, when a predator must divide its attention between the different cryptic prey types available, its search becomes less efficient than if it were instead focusing on a single prey type. It must therefore carefully allocate its attention such that it maximizes the likelihood of finding food and avoiding predators (Clark & Dukas 2003). When a task is relatively simple limited attention is no longer such a constraining factor. For example, blue jays (*Cyanocitta cristata*) are much less likely to detect a peripheral target (akin to an approaching predator) displayed on a computer monitor when the central search task is difficult rather than easy (Dukas & Kamil 2000). Similarly, if multiple conspicuous prey types are available, a predator maximizes its energy intake by dividing attention equally among all prey types, whereas when the prey are cryptic, a predator does best by focusing attention on a single prey type (Dukas & Ellner 1993). This enhanced performance when focusing on a single cryptic prey type is the basis for the search image hypothesis. Tinbergen (1960) noted that great tits (*Parus major*) foraging for insect larvae captured the most common prey disproportionately more often than would have been expected given their abundance in the environment, and overlooked rarer prey items. He suggested that repeated capture of the most common cryptic prey type enhances detection as the predator forms a mental representation of the prey and its distinguishing features. Numerous examples exist in the literature of predators overselecting the most common cryptic prey and of enhanced performance following recurring capture of the same cryptic prey type (Bond 1983, Gendron 1986, Bond & Riley 1991, Reid & Shettleworth 1992, Langley 1996, Bond & Kamil 1999). This negative frequency-dependent selection by predators favoring the survival of rare cryptic prey (also called apostatic selection) has been demonstrated both in the lab and in the field, and maintains and enhances prey polymorphism as well as increasing overall prey crypticity (Bond & Kamil 1998, 2002, Olendorf et al. 2006).

There have been relatively few studies to date on the effects of cryptic prey on social predators, but it appears that it has an even greater negative effect than on solitary predators. Courant & Giraldeau (2008) found that when feeding on cryptic seeds in the presence of a conspecific, nutmeg mannikins (*Lonchura punctulata*) eat fewer seeds and are less accurate than when feeding alone; this effect of conspecific presence does not occur when seeds are conspicuous. Furthermore, they found that the negative effects of the presence of another bird persist even when the conspecific is subsequently removed. They suggest that self-imposed costs in the presence of a conspecific or interference with search image acquisition due to the monitoring of others makes foraging for cryptic prey more difficult for social predators. However, Courant & Giraldeau's (2008) study did not look at an additional aspect of social foraging. For animals that feed in groups, each individual can choose between two alternative foraging tactics: searching for food, the producer tactic, or searching for other group members that have found food in order to join them, the scrounger tactic. When the two tactics are mutually exclusive, when an individual cannot search for food and scrounging opportunities simultaneously, the group conforms to a producer-scrounger (PS) game (Barnard & Sibly 1981, Vickery et al. 1991, Caraco & Giraldeau, 1991). The PS game has been documented in both laboratory (Giraldeau et al. 1990, 1994, Mathot & Giraldeau 2008) and field experiments (Barnard & Thompson 1985, Ha & Ha 2003, Morand-Ferron et al. 2007).

Individuals within a PS game can make exclusive use of one tactic, or as is more often observed, can alternate between producing and scrounging (Giraldeau et al. 1990, Giraldeau et al. 1994, Koops & Giraldeau 1996, Beauchamp 2001). Because scroungers do not actively contribute to the discovery of new food patches, the pay-offs to each tactic are negatively frequency-dependent on the frequency of scrounger use within the group. When scrounging is rare, scroungers do better than producers as there are many joining opportunities to be shared between few scroungers. When scrounging is more common, scroungers fare worse than producers because fewer discoveries must be divided amongst the numerous scroungers. The frequency-dependence of payoffs eventually leads to a stable equilibrium frequency of scrounger use, where the relative payoffs to both tactics are equal (Mottley & Giraldeau 2000). Many factors have been empirically shown to affect the stable equilibrium frequency of scrounger in a group, such as group size (Coolen 2002), dominance status (Liker & Barta 2002), predation risk (Barta et al. 2004, Mathot & Giraldeau 2008), energetic state (Lendvai et al. 2004), as well as prey crypticity (Barrette & Giraldeau 2006).

For groups of animals engaged in a PS game, the longer detection times and slower search speeds caused by foraging on cryptic prey should be felt equally for individuals engaged in both the producer and scrounger tactics. Producers will be slower to discover new patches, but because scroungers ultimately rely on them for their own feeding opportunities, the lower feeding rates attributable to cryptic prey will be experienced by all group members. Conversely, the time and energy costs of more frequent detection errors when searching for patches of cryptic prey are felt exclusively by producers. Although group members engaged in both tactics can make detection errors when searching for individual food items located within a patch found by a producer, only producers will make patch-level detection errors as they actively search for clumps of food. These higher costs to producing when prey are cryptic should cause a shift towards increased equilibrium frequency of the scrounger tactic within a group. Indeed, Barrette & Giraldeau (2006) found that when groups of nutmeg mannikins search for cryptic white millet seeds, the stable equilibrium frequency of scrounger increases, presumably because of more frequent producer-specific detection errors. If the producer-specific costs of detection errors do indeed lead to an increase in scrounging, then a greater number of detection errors should bring about an even larger increase in scrounger tactic use. Foragers make more frequent detection errors when searching for multiple cryptic prey types than a single cryptic prey type because of the effects of divided attention (Dukas & Kamil 2001), making this an effective means of verifying the hypothesis that more frequent detection errors further increase scrounger use. Moreover, because prey polymorphism is common in cryptic species (Bond 2007), and because many cryptic prey species have overlapping distributions (e.g. moths, Endler 1984), the effect of multiple cryptic prey types on social foraging tactic use is highly relevant.

Classic studies exploring the effects of cryptic prey have successfully used granivorous birds feeding on colored grains on various backgrounds as a model system (Dawkins 1971a, b, Bond 1983, Reid & Shettleworth 1992). Therefore, in order to determine how the presence of multiple cryptic prey types affects tactic use in social predators engaged in a PS game, we tested groups of nutmeg mannikins searching for one or two colors of millet seed, and made seeds cryptic or conspicuous by changing the background on which the birds searched. We expect birds to be less efficient when prey are cryptic than when conspicuous, and to see a further decrease in foraging efficiency when two prey types are available, but only when they are cryptic. In addition, birds should scrounge more when prey are cryptic, and further increase their scrounger use when two cryptic prey types are available relative to when one is available due to the producer-specific costs of more frequent detection errors. We do not expect birds to adjust scrounging behavior in response to multiple conspicuous prey types.

METHODS

Subjects

Nutmeg mannikins are small passerine birds native of south-east Asia. They are non-aggressive, sexually monomorphic granivores that forage in flocks throughout the year (Immelmann 1982), typically feeding on seeds taken from the ground or directly from grass stalks (Goodwin 1982). For the experiment, 20 individuals of unknown sex from a colony of 25 wild-caught nutmeg mannikins were randomly assigned to four flocks of five birds each. Each flock was placed in an indoor aviary (1.5 × 3.8 × 2.3 m high) and kept at temperatures of 21-23°C on a 12:12 h light:dark photoperiod. Individual birds were identified with unique combinations of colored leg bands. Outside experimental periods, birds had ad libitum access to a mixture of red, white, golden and Siberian millet seeds as well as to the experimental seeds. Water was offered ad libitum at all times, and a bath was available outside experimental periods.

Foraging Substrate

Flocks foraged on a 1.07 x 1.22 m grid consisting of a plywood board onto which a white PVC trellis was firmly fixed. The trellis effectively partitioned the grid into 434 numbered 2.5 cm^2 potential food patches. Experimental seeds consisted of white millet seeds without husks dyed red and yellow using food coloring (Club House Food Colour Preparation, McCormick Canada, London, Canada). The background of the grid consisted of pearl barley secured to the plywood board with all-purpose glue (Ross All Purpose White Glue, Ross Products, Toronto, Canada). To create the background, the trellis was placed on the plywood board, and the openings in the trellis were traced onto the board with a pencil. The trellis was then removed, and barley was glued in each patch outline, one patch at a time: a generous amount of wood glue was spread in the patch, and a pinch of barley was dropped into the glue and flattened as much as possible, adding pieces of barley to fill in any holes. In order to adjust the crypticity of the experimental seeds, the background barley was painted using matte water-based acrylic paint (Deserres Student Grade Acrylic Paint in Carbon Black, Rubine Red and Bright Yellow, Deserres, Montréal, Canada). For the conspicuous grid, all the barley on the background was painted black once it was glued to the plywood board; for the cryptic grid, half the barley was painted red and the other half painted yellow. These two types of barley were then mixed before being glued to the board. The red and yellow paints were chosen to match the colors of the dyed experimental seeds as closely as possible, appearing identical to the human eye. The barley of both grid types was then covered with a coat of satin finish water-based wood varnish (Varathane Diamond Wood Finish, Tremco, Toronto, Canada) prior to placement of the trellis. The grids were placed on a table and rested 90 cm off the aviary floor, at a seated observer's eye level. Outside trial periods, the grids were covered by an opaque plastic cover.

Training

The entire training and testing sequences for this study are summarized in Figure 1. Flocks were first given a 3 d period to adjust to the aviary. During this time, two separate dishes containing the experimental seeds and millet seed mixture were placed directly on the covered foraging grids. Birds were food deprived for 12.5 h starting in the evening of day 3: food was removed at lights off overnight. This period of food deprivation was used throughout the experiment, and was necessary because nutmeg mannikins store seeds in their crops overnight.

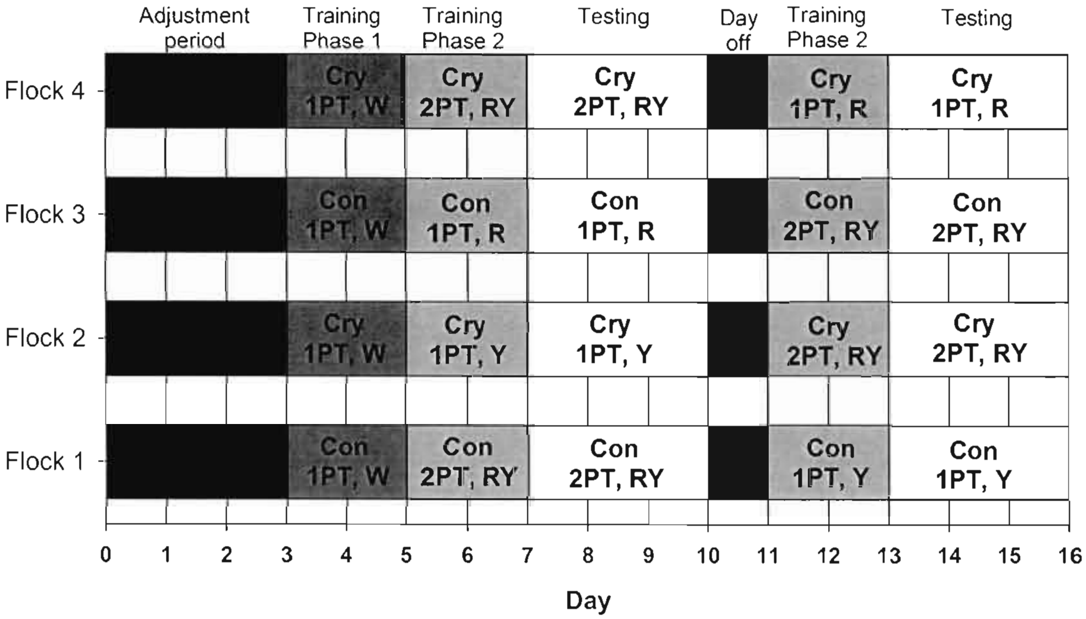

Figure 1: Sequence of training and testing periods for flocks of nutmeg mannikins feeding on white (W), red (R), yellow (Y), or red and yellow (RY) millet seeds on foraging grids on which the seeds appeared conspicuous (Con) or cryptic (Cry). The one prey type and two prey type conditions are referred to as 1PT and 2PT, respectively. At the end of day 16, the foraging grids were switched for the alternative type (conspicuous or cryptic) and the sequence was repeated from days 17 to 32.

The first phase of training began on the morning of day 4. On days 4 and 5, flocks foraged on the grids for 20 patches of 10 white millet seeds without husks, placed in randomly-selected patches of the grid. This first phase of training allowed the birds to forage on the grids without the added difficulty of the colored experimental seeds. For phase 1 training trials, the plastic cover was removed for 10 min, after which all food remaining on the grid was removed and the plastic cover replaced. These nutmeg mannikins were highly neophobic, and this trial duration was necessary for the first phase of training in order to allow the birds ample time to use the foraging grids. Five phase 1 training trials were conducted on days 4 and 5, at 1 h intervals.

The second phase of training, on days 6 and 7, had flocks searching the grids for the red and yellow experimental seeds under the same conditions in which they would be subsequently tested. For flocks in the one prey type condition (hereafter referred to as 1PT), 10 seeds of a single type (red or yellow) were placed in each of 20 randomly-selected patches. For flocks in the two prey types condition (2PT), 10 red seeds were placed in each of 10 randomly-selected patches as well as 10 yellow seeds in 10 randomly-selected patches. Five phase 2 training trials were conducted per day at 1 h intervals: a phase 2 training trial started when the plastic cover was removed from the grid, and ended when no patch discoveries had been recorded for 1 min. All remaining food was then removed, and the grid cover replaced.

Testing

Test trials began on the morning of day 8. A test trial began when the first bird landed on the grid, and ended when the flock failed to make any patch discoveries for 1 min. As in the second phase of training, flocks in the 1PT condition searched for 20 randomly-selected patches each containing 10 seeds of a single type, while flocks in the 2PT condition searched for 20 randomly-selected patches, half containing 10 yellow seeds, and half containing 10 red seeds. Five trials were conducted each day at hourly intervals, and flocks were tested for 3 d (days 8, 9 and 10). A different focal individual was observed for each trial, such that each flock member was observed once per day. The focal individual was chosen randomly, with the provision that each bird was never observed at the same time over the 3 d of testing. Trials were videotaped through a one-way mirror using a Panasonic DMC-FZ7 digital camera (Matsushita Electric Industrial Co. Ltd., Osaka, Japan), and the experimenter (S.S. or K.M.) vocally identified all birds and indicated the location of the focal bird throughout a trial. If a flock failed to land on the foraging grid within 1 min of it being uncovered, the cover was replaced, and the trial was restarted 5 to 10 min later (the time taken to run a trial with another flock), at which time the birds would invariably land and commence foraging. Flocks were provided with ad libitum food at the end of day 10, and no testing was conducted on day 11. On days 12 to 16, the birds experienced the same sequence of training and testing trials as days 6 to 10, with the alternative number of prey types (1PT or 2PT). At the end of day 16, the foraging grid was switched to the alternative type (cryptic or conspicuous), and the sequence of days 1 to 16 was repeated from days 17 to 32. All flocks were tested on both the cryptic and conspicuous grids, with both one and two prey types available. The order of the experimental conditions was balanced across flocks, and two randomly-chosen flocks were tested with red seeds for the 1PT condition, while the other two were tested with yellow seeds.

Recording Behavior

The observer (S.S.) recorded behavior from video playbacks of trials using the event recorder software Noldus Observer Video-Pro 5.0 (Noldus Information Technology, Wageningen, The Netherlands). A focal bird's grid time consisted of the period of a trial during which it was on the foraging grid, beginning when it landed on the foraging grid and ending after its last feeding event. Grid time excludes short periods when the focal individual temporarily left the grid to return to the perches. Five events were recorded:

(1) producing a patch.
(2) scrounging a patch.
(3) eating a seed from a patch that was produced.

(4) eating a seed from a patch that was scrounged.
(5) making a detection error: a peck in a patch that never contained food.

A focal bird "produced" a patch when it fed from an unattended patch, and "scrounged" a patch when it fed from a patch from which other birds were feeding or had just fed. From the above five directly observed events, we calculated for the focal bird:

(1) number of patches exploited (produced and scrounged) per trial.
(2) number of seeds eaten (produced and scrounged) per trial.
(3) patch exploitation rate: the number of patches exploited per minute of grid time.
(4) feeding rate: the number of seeds eaten per minute of grid time.
(5) number of detection errors per trial.
(6) proportion of seeds scrounged: the number of seeds scrounged divided by the total number of seeds eaten during a trial.
(7) proportion of patches scrounged: the number of patches scrounged divided by the total number of patches exploited during a trial.

Statistical Analyses

We built linear mixed-effects models (LME) using R v. 2.7.0 (R Development Core Team 2008) to determine if behavior was affected by prey crypticity and the number of prey types available. Our four flocks of birds were repeatedly tested under the same experimental conditions, and so we used LME which accounts for the non-independence of errors created by spatial and temporal pseudoreplication (Crawley, 2007). In the models, we included 'Crypticity' (cryptic or conspicuous prey), 'Prey Types' (1PT or 2PT) and their interaction as fixed effects, as well as flock, bird ID nested within flock, and day nested within ID nested within flock as random effects. All non-significant interactions ($p > 0.05$) were removed from the models. Prior to analysis, proportion data were arcsine square-root transformed, and the Poisson-distributed detection error data were $\ln(n+1)$ transformed. All values are reported as the mean ± SEM.

RESULTS

General

Data were collected from 240 test trials, for a total of 280.25min of grid time for focal birds. The number of patches exploited per trial (Fig. 2a) was not affected by prey crypticity ($F_{1,178} = 0.42$, $p = 0.52$) or by the number of prey types available ($F_{1,178} = 0.67$, $p = 0.41$), nor was there an interaction (patches/trial: conspicuous 1PT: 7.22 ± 0.41; conspicuous 2PT: 6.93 ± 0.36; cryptic 1PT: 6.98 ± 0.42; cryptic 2PT: 6.78 ± 0.37; Crypticity × PT: $F_{1,177} = 0.020$, $p = 0.89$; Fig. 2a). Birds ate significantly fewer seeds per trial (Fig. 2b) when prey were cryptic than when conspicuous ($F_{1,178} = 14.93$, $p = 0.0002$). However, the number of prey types available had no effect on the number of seeds eaten per trial ($F_{1,178} = 1.14$, $p = 0.29$), and there was no interaction (seeds/trial: conspicuous 1PT: 36.53 ± 1.99; conspicuous 2PT: 36.30 ± 1.89; cryptic 1PT: 32.52 ± 2.21; cryptic 2PT: 29.87 ± 1.15; Crypticity × PT: $F_{1,177} = 0.80$, $p = 0.37$; Fig. 2b).

Foraging Efficiency

There was a significant interaction between prey crypticity and number of prey types available for grid time (Crypticity × PT: $F_{1,177} = 4.34$, $p = 0.039$; Fig. 3a). Under conspicuous conditions, grid times were shorter and remained similar in duration regardless of the number of prey types (conspicuous 1PT: 56.54 ± 2.95 s; conspicuous 2PT: 56.01 ± 4.12 s), whereas grid times were longer under cryptic conditions and were longest when two cryptic prey types were available (cryptic 1PT: 76.73 ± 5.82 s; cryptic 2PT: 90.97 ± 5.68 s; Fig. 3a). The main effect of crypticity on grid time was highly significant ($F_{1,177} = 60.49$, $p < 0.0001$), but the overall effect of number of prey types was just short of statistical significance ($F_{1,177} = 3.75$, $p = 0.055$).

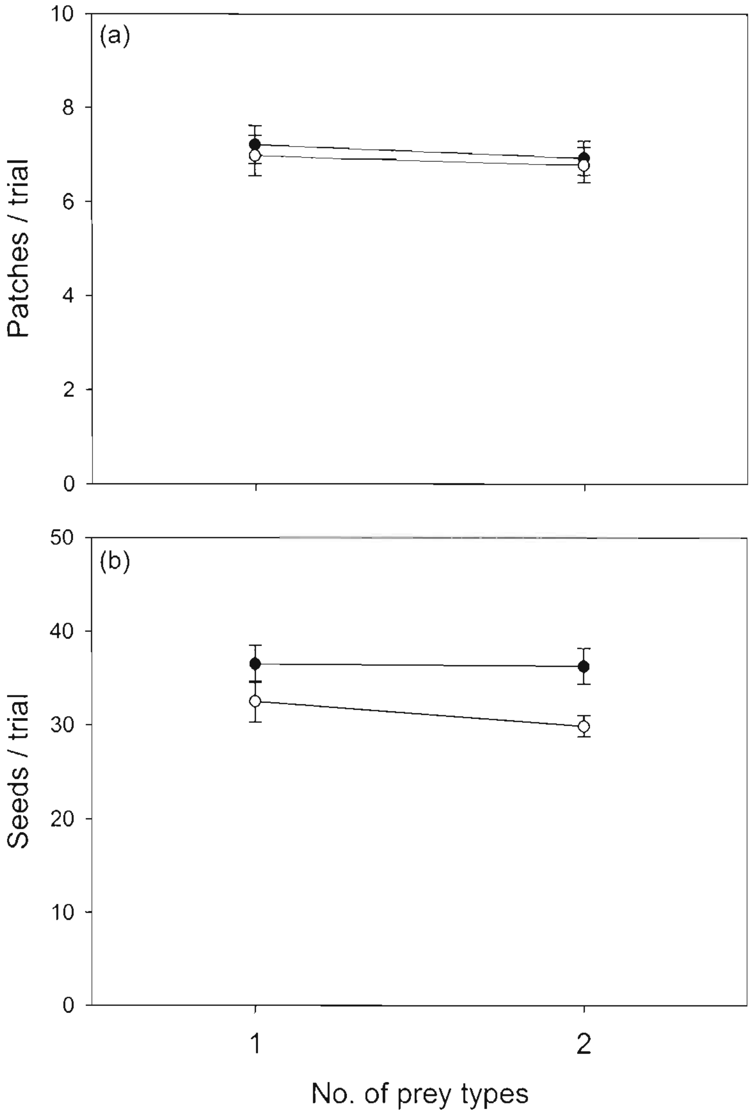

Figure 2: Mean ± SE (a) patches exploited per trial (b) seeds eaten per trial for nutmeg mannikins searching for one or two prey types under conspicuous (black circles) or cryptic (white circles) conditions.

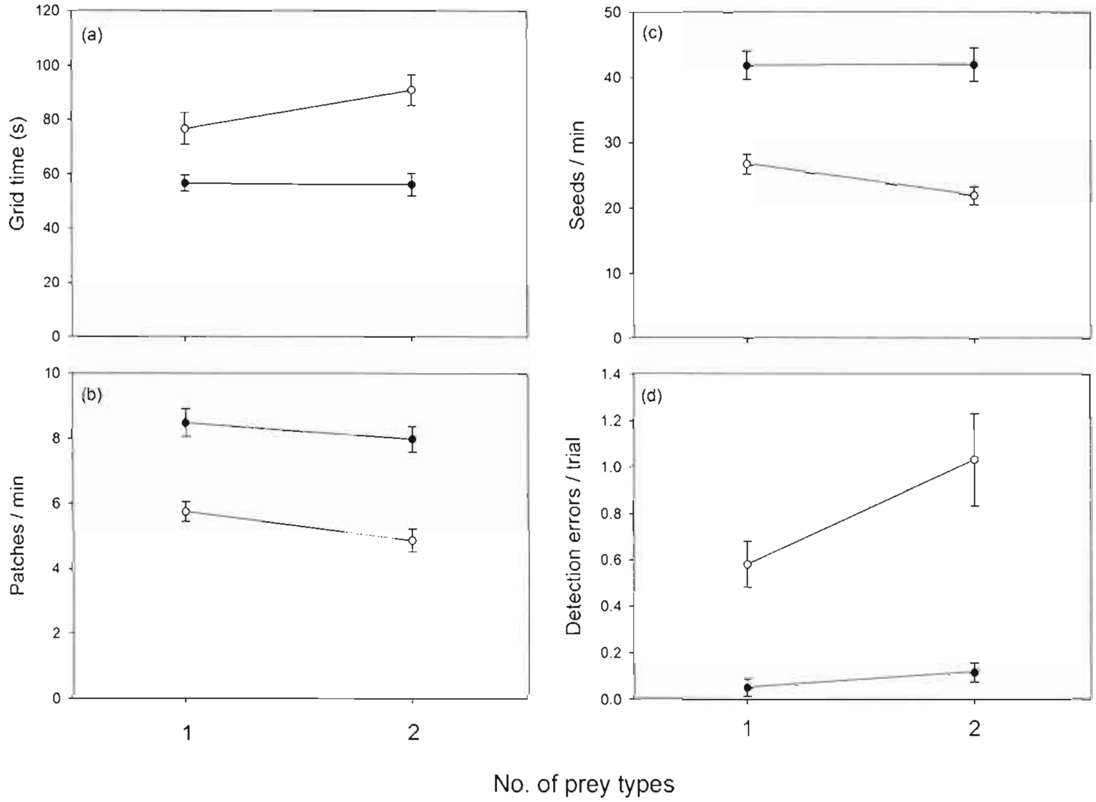

Figure 3: Mean ± SE (a) grid time (b) patch exploitation rate (c) feeding rate (d) detection errors made per trial for nutmeg mannikins searching for one or two prey types under conspicuous (black circles) or cryptic (white circles) conditions.

There was no interaction between prey crypticity and number of prey types available for patch exploitation rate (patches/min: conspicuous 1PT: 8.48 ± 0.44; conspicuous 2PT: 7.98 ± 0.40; cryptic 1PT: 5.75 ± 0.30; cryptic 2PT 4.87 ± 0.36; Crypticity × PT: $F_{1,177} = 0.52$, $p = 0.47$; Fig. 3b). However, birds exploited significantly fewer patches per minute when prey were cryptic than when prey were conspicuous ($F_{1,178} = 123.97$, $p < 0.0001$), and fewer when two prey types were available than when only one prey type was on the foraging grids ($F_{1,178} = 6.98$, $p = 0.009$).

The interaction between prey crypticity and number of prey types available was significant for feeding rate (Crypticity × PT: $F_{1,177} = 4.71$, $p = 0.031$; Fig. 3c): feeding rates were consistently high when prey were conspicuous (seeds/min: conspicuous 1PT: 41.89 ± 2.12; conspicuous 2PT: 42.07 ± 2.54), but decreased when prey were cryptic, particularly when two prey types were available (seeds/min: cryptic 1PT: 26.75 ± 1.52; cryptic 2PT: 21.94 ± 1.33). The overall effects of crypticity ($F_{1,177} = 234.95$, $p < 0.0001$) and number of prey types ($F_{1,177} = 4.06$, $p = 0.045$) were also significant. The effect of prey crypticity on the number of detection errors per trial (Fig. 3d) did not vary with the number of prey types available (detection errors/trial: conspicuous 1PT: 0.05 ± 0.04; conspicuous 2PT: 0.12 ± 0.04; cryptic 1PT: 0.58 ± 0.10; cryptic 2PT 1.03 ± 0.20; Crypticity × PT: $F_{1,177} = 2.01$, $p = 0.16$; Fig. 3d). The number of detection errors per trial did however increase when prey were cryptic versus conspicuous ($F_{1,178} = 61.11$, $p < 0.0001$), and when two prey types were available versus only one prey type ($F_{1,178} = 6.08$, $p = 0.015$).

Scrounging Behavior

There was a significant interaction between prey crypticity and the number of prey types available in regards to the proportion of seeds scrounged (Crypticity × PT: $F_{1,177} = 4.71$, $p = 0.04$; Fig. 4a). Birds increased their overall use of the scrounger tactic when prey were cryptic relative to conspicuous, but the effect of the number of prey types available on scrounging behavior differed according to prey crypticity. Increasing the number of prey types caused a slight increase in scrounging behavior when prey were cryptic, whereas birds reduced scrounging when two conspicuous prey types were available versus only one prey type (proportion of seeds scrounged: conspicuous 1PT: 0.26 ± 0.028; conspicuous 2PT: 0.22 ± 0.037; cryptic 1PT: 0.30 ± 0.051; cryptic 2PT: 0.32 ± 0.057; Fig. 4a). The main effects of crypticity ($F_{1,177} = 2.73$, $p = 0.10$) and number of prey types ($F_{1,177} = 1.46$, $p = 0.23$) were not significant.

Results were qualitatively similar for the proportion of patches scrounged (Fig. 4b). However, the interaction between prey crypticity and number of prey types available was not significant (proportion of patches scrounged: conspicuous 1PT: 0.37 ± 0.031; conspicuous 2PT: 0.31 ± 0.040; cryptic 1PT: 0.43 ± 0.054; cryptic 2PT 0.46 ± 0.060; Crypticity × PT: $F_{1,177} = 2.00$, $p = 0.16$; Fig. 4b). The main effect of crypticity was significant ($F_{1,178} = 9.90$, $p = 0.0019$), while the number of prey types available did not have an overall effect ($F_{1,178} = 0.045$, $p = 0.83$).

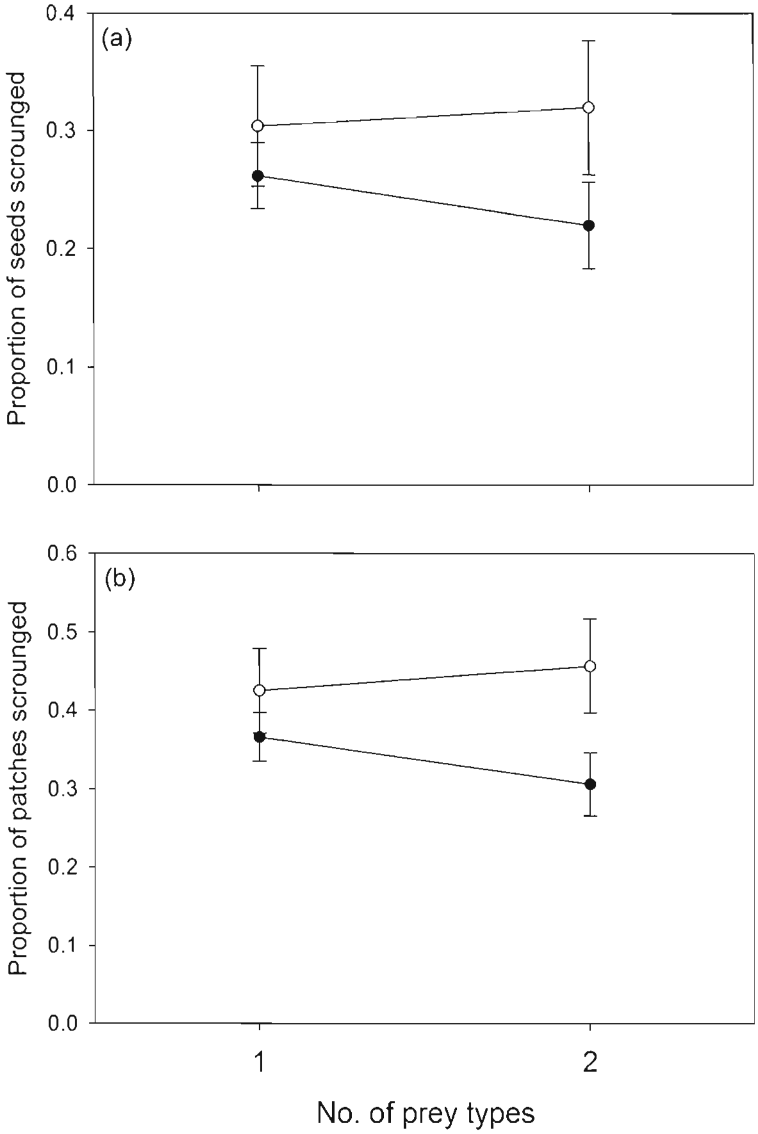

Figure 4: Mean ± SE (a) proportion of seeds scrounged (b) proportion of patches scrounged for nutmeg mannikins searching for one or two prey types under conspicuous (black circles) or cryptic (white circles) conditions.

DISCUSSION

Nutmeg mannikins had greater difficulty feeding on the cryptic seeds than on the conspicuous seeds: grid time was longer, patch exploitation and feeding rates were lower, and birds made more detection errors per trial. This indicates that the colored experimental seeds were indeed made to be cryptic on the matching foraging substrate. Similarly, we found that birds were less efficient when foraging on two cryptic prey types versus one cryptic prey type, as patch exploitation and feeding rates decreased while grid time and frequency of detection errors increased. This suggests that the effect of crypticity was additive, as would be expected by dividing attention between different prey types (Dukas & Kamil 2001). This is the first study to demonstrate the negative effects of multiple cryptic prey types on foraging efficiency for social predators. We found also that birds made more detection errors and had lower patch exploitation rates when two conspicuous prey types were available compared to one conspicuous prey type. However, there was no change in grid time or feeding rate from one to two conspicuous prey types. Although attentional constraints should not be an issue when prey are conspicuous (Dukas 2002, Bond & Kamil 2006), these results are consistent with divided attention operating at the level of patch exploitation, and may thus be related to foraging on a clumped food distribution in a PS game.

The longer grid times observed under cryptic conditions could have resulted from a greater difficulty in finding patches, finding seeds within patches, or both. Nutmeg mannikins exploited a similar total number of patches per trial regardless of the number of prey types available and their crypticity. But despite having exploited a similar number of patches, they ate significantly fewer seeds when prey were cryptic, and there was a tendency for a further reduction in seed consumption when two cryptic prey types were available. Thus, it proved more difficult to locate the seeds within a cryptic patch than within a conspicuous patch, with a slight increase in difficulty when there were multiple cryptic prey types present; birds must have left cryptic patches before all 10 seeds had been eaten. Considered alone, this difference between number of patches and number of seeds exploited across experimental conditions would suggest that longer grid times under cryptic conditions were a result of a greater difficulty to locate seeds. However, nutmeg mannikins also had lower patch exploitation rates when prey were cryptic, exploiting fewer patches per minute of grid time, with a further decrease when two prey types were available. Therefore both locating patches and locating seeds within them were challenging for the birds and contributed to longer grid times, although given our data there is no way for us to determine their relative importance.

We might not have obtained these results if heterogeneous patches containing both red and yellow seeds had been used in the two prey types condition instead of the homogeneous patches. Perhaps locating patches would have become less challenging relative to locating seeds within patches, because birds could focus on searching for a single type of patch but would have to divide their attention between both seed types in the patch (Dukas & Kamil 2001). The presence of two cryptic prey types would then not have affected patch exploitation rate, and the decrease in number of seeds eaten from one to two cryptic prey types would have been even greater than what we observed.

Nutmeg mannikins foraging in a PS game increased their use of the scrounger tactic when prey were cryptic, as would be predicted if crypticity imposed producer-exclusive costs (Barrette & Giraldeau 2006). Birds made more frequent detection errors under cryptic conditions, and so these producer-specific costs likely led the birds to reduce their investment in this tactic. Although this effect might appear modest, it is consistent and significant, as Barrette & Giraldeau (2006) found similar results. In addition, our results suggest a further increase in scrounger use when two cryptic prey types were available, perhaps caused by the greater number of detection errors under this experimental condition. This latter increase in scrounging was however quite small compared to the overall increase from conspicuous to cryptic conditions. In both cases, higher scrounger use may have reflected the magnitude of the increase in number of detection errors. Birds made 1.8 times more detection errors per trial when two cryptic prey types were available versus one cryptic prey type. Comparatively, when going from conspicuous to cryptic prey, birds made 11.6 and 8.6 times more detection errors in the one prey type and two prey types conditions, respectively. Although not conclusive, our results suggest that more frequent detection errors lead to decreased producer use: a smaller increase in the frequency of detection errors led to a smaller decrease in producing. This effect could be further explored by rendering the producing task more difficult by even further dividing attention, for instance by adding a third prey type or by making the background more complex (Merilaita 2003, Bond & Kamil 2006). A corresponding increase in the number of detection errors and decrease in producing would possibly be observed in response. Such a reduction in the use of producer was also found in a study that experimentally manipulated producer-exclusive costs by increasing the effort required to find food in groups of nutmeg mannikins (Giraldeau et al. 1994). It is thus clear that foragers adjust tactic use in response to changing costs of playing producer.

Unexpectedly, nutmeg mannikins reduced their scrounging when two conspicuous prey types were present relative to one conspicuous prey type. It is unclear why birds adjusted their tactic use in response to the number of conspicuous prey types. The birds responded as though producing became more profitable when two conspicuous prey types were present, or alternatively that scrounging became more costly. This could be related to the observed increase in the number of detection errors and decrease in patch exploitation rates under the conspicuous two prey types condition, although we can think of no reason why this would be the case. Our data do not permit us to further explore this result, but it undeniably requires further study.

The results of our study have a number of broad implications for both social foragers and their prey. When prey are cryptic, a group of foraging predators will have a lower collective rate of prey exploitation due to higher levels of scrounging. Individuals engaged in the scrounger tactic do not contribute to the discovery of new food patches, and therefore do not make food resources available to the group (Coolen 2002). This can lead to lower growth rates and promote stability of predator populations, which in turn allows prey populations to exist at higher densities (Coolen et al. 2007). Lower food discovery rates in a group of predators also lower predation pressure on prey. Cryptic coloration is an efficient means of avoiding detection by solitary predators, and this seems to be even truer when the predators are social foragers. Moreover, if predators further increase their scrounger use when multiple cryptic prey types are present, there is an added anti-predatory advantage for polymorphic cryptic prey of social predators. Our results and those of Barrette & Giraldeau (2006) indicating higher scrounger use on cryptic prey, coupled with the results of Courant & Giraldeau (2008) who found reduced foraging efficiency on cryptic prey in the presence of a competitor, imply that social foragers would do better to avoid cryptic prey that solitary foragers could more readily exploit.

Our results would also suggest that prey polymorphism or the presence of multiple different prey types will have different effects on social predators depending on prey crypticity: when prey were conspicuous, groups shifted towards more producing, in opposition to the small increase in scrounger use when prey were cryptic. With more group members actively searching for food as producers, groups could become more efficient when feeding on multiple conspicuous prey types, and this higher predation pressure should then cause polymorphism to be selected against for conspicuous prey. Conversely, polymorphism in cryptic prey should be favored by selection via search image formation and apostatic selection by predators for common cryptic prey types (Bond & Kamil 2002), and by lower predation pressure due to divided attention (Dukas & Kamil 2001) and higher scrounger use. Color polymorphism seems in fact to be more common in cryptic than in conspicuous prey species, and has been recorded in cryptic mollusks, insects, spiders, crustaceans and vertebrates (Bond & Kamil 2006, Bond 2007). Our study suggests that polymorphism may have evolved to a much lesser extent in conspicuous prey species than in cryptic prey species in partial response to differences in social predator foraging tactic use.

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GENERAL CONCLUSION

Our experiment is one of the relatively few studies to examine the effects of cryptic prey on social predators, after Barrette & Giraldeau (2006) and Courant & Giraldeau (2008). It is, however, the first to also analyze the effects of multiple cryptic prey types on socially foraging animals. Our results indicate that social predators respond to the presence of multiple cryptic prey types in a similar manner to solitary predators, with a reduction in foraging efficiency via lower feeding rates and more frequent detection errors. Thus, the constraints of limited attention likely also exist in a group foraging context, and dividing attention between different cryptic prey types leads to reduced efficiency.

Beyond this study, the effects of limited attention have not been explored for social foragers. Being engaged in a producer-scrounger game could in itself lead to divided attention and reduced foraging efficiency of predators. Producing and scrounging are incompatible foraging tactics, meaning a predator should effectively divide its attention when alternating between the two tactics. Because performing particular tasks activates certain regions of the brain while suppressing others (Dukas 2002, 2004), it is possible that a predator will be less efficient when switching between producing and scrounging than when using only one of the two tactics. This may be exacerbated when the producing task is cognitively difficult, such as searching for multiple cryptic prey types, as attention is even further divided by the demanding search task.

Furthermore, it is not known if limited attention causes foragers in a producer-scrounger game to form search images in order to improve their detection ability. Our study does not permit us to test for this: while we used a 1:1 ratio of the two prey types, a search image is defined as an increase in detection ability through repeated capture of the most common cryptic prey type (Tinbergen 1960), and there is empirical evidence that search images will in fact only be formed when one prey type is in the majority (Bond 1983). If cryptic prey types are present in a more skewed ratio, it is possible that group members will form a search image and focus their producing effort on the more common prey type.

Scrounging an alternative type could then interfere with this search image and reduce their efficiency when playing producer, just as searching for an alternative prey type prevents the maintenance of a search image for solitary predators (Plaisted & Mackintosh 1995). An unequal ratio of cryptic prey types could also create skill pools within groups, where frequency-dependent learning of foraging specializations (search images in this case) allows individuals to increase their diet diversity by maintaining their specialization as producers while concurrently benefiting from the specializations of others by scrounging their discoveries (Giraldeau 1984). These are interesting avenues to pursue in future research.

This study also confirms the results of Barrette & Giraldeau (2006), that groups of predators foraging in a producer-scrounger game increase their use of the scrounger tactic when prey are cryptic. This is likely caused by the producer specific costs of more frequent detection errors. While a large increase in the number of detection errors from conspicuous to cryptic prey corresponds to a large increase in scrounging, a smaller increase in the number of detection errors from one to two cryptic prey types is accompanied by a smaller increase in scrounging.

If the producing task were more challenging, it is possible that producers would make even more frequent detection errors and a larger increase in scrounger use would be observed. This could be accomplished by further dividing attention between additional cryptic prey types. Alternatively, a more complex foraging substrate could be used. There is convincing evidence that when a background is more complex, composed of a wide range of elements, searching for cryptic prey is more difficult (Bond & Kamil 2006). A background that is more complex has more information to visually process, and thus requires a more exhaustive and protracted search (Merilaita 2003, Bond 2007). Enhancing the constraints of limited attention by using a greater variety of shapes, sizes and colors when composing the foraging background could thus lead individuals in a producer-scrounger game to adjust their tactic use.

Unexpectedly, we also found that social predators increase their use of the producer tactic when multiple conspicuous prey types are available relative to one conspicuous prey type. This would suggest that producing becomes more profitable when many conspicuous prey types are present, or that scrounging becomes more costly. If birds develop a bias for one prey type based on a perceived pay-off difference between the prey, this could potentially lead to an increase in producing. To ensure consumption of the prey type the birds consider more profitable, they would have to adopt the producer tactic, as the diet composition of scroungers is ultimately dependent on the choices made by producers; producing is then perceived as the more profitable tactic. However, we cannot test this hypothesis given our data due to the relatively small number of patches exploited per observation. Moreover, a bias for one prey type could equally have been formed under cryptic conditions, and we observed a small decrease in producing when prey were cryptic. Regardless, this result certainly merits further study.

This study has a number of broad implications for socially foraging predators and their prey. Our results, along with those of Barrette & Giraldeau (2006) and Courant & Giraldeau (2008), indicate that prey crypticity may be a more effective anti-predator strategy against social predators than against solitary predators. When prey are cryptic, group members make greater use of the scrounger tactic, thereby lowering collective food discovery rates as scroungers do not contribute to the detection of new food patches. When multiple cryptic prey types are present, this effect may be even greater given a further increase in scrounger use. Lower foraging efficiency may thus lead social predators to avoid certain cryptic prey types that solitary predators will more readily exploit. Moreover, crypsis may be a more commonly-used predator avoidance strategy for prey when their predators are social than when they are solitary.

In addition, our results indicate that the effect of prey polymorphism on social forager tactic use depends on prey crypticity. An increase in producing should cause polymorphism to be selected against when prey are conspicuous; as more individuals actively search for food, groups of predators will experience higher collective rates of food discovery. Conversely, selection should favor polymorphism when prey are cryptic because of higher scrounger use and lower collective food discovery rates. Polymorphism is indeed quite common in cryptic prey species (Bond 2007), and this has largely been attributable to search image formation and apostatic selection by predators for common cryptic prey types (Bond & Kamil 2002). However, our results suggest that differences in social foraging tactic use may also contribute to the greater prevalence of polymorphism in cryptic prey species.

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