Escape and Vocal Responses of Eastern Chipmunks (Tamias striatus) to Simulated Aerial Predator Attack

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Abstract

The behaviours of eastern chipmunks (*Tamias striatus*) in response to aerial predators were studied in the field using trained kestrels (*Falco sparverius*) flying over a food patch where animals of known gender, age and burrow location categories were foraging. Their typical response was to flee toward a nearby refuge while producing a trill. After a few seconds, chipmunks usually emerged and started to produce long (but sometimes interrupted) series of chucks while facing the predator. Acoustical analysis showed that the trill consisted of a rapid series of usually high pitched and variable notes while most chucks consisted of two partially overlapping components differing mainly in frequency range. No differences were observed between individuals of different categories for most antipredator responses. Various observations suggest that the trill functions to startle the predator and that the chuck deters the predator from hunting in the area.



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Résumé

Nous avons étudié les comportements des tamias rayés (Tamias striatus) en présence d'un prédateur aérien à l'aide de crécerelles américaines (Falco sparverius) volant au-dessus d'une source de nourriture où des animaux regroupés selon le sexe, l'âge et la distance au terrier se ravitaillaient. Leur réponse typique était de fuir vers un refuge à proximité en produisant un trill. de réapparaître après quelques secondes puis de produire une longue série de chucks en faisant face au prédateur. Une analyse acoustique révéla que le trill consiste en une série rapide de différentes lotes et que la majorité des chucks consistent en deux composantes de fréquence différente. Aucune différence n'a été observée entre les différents regroupements pour la majorité des variables observées. Diverses observations suggèrent que le trill a pour but de surprendre le prédateur et que le chuck le dissuade de chasser dans les environs.

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Introduction

Predation is an important selective force in many populations of animals, and predation risk is a major influence on animal behaviour (Lima & Dill, 1990). Although a great number of antipredator strategies exist (Edmunds, 1974), they can be broadly divided into escape response, defence and alarm signals (Curio, 1976). Two of the most widespread are fleeing when predators come too close and calling when potential predators are nearby.

Animals are expected to use antipredator strategies that will maximize their probability of survival (Buchanan et al. 1988; Cresswell, 1993). They should select a particular strategy according to conditions of the encounter such as magnitude of a threat and presence of relatives that would be affected by a particular response. Factors such as age, gender and familiarity with the area are likely to correlate with strategies through their effects on encounter risk and presence of relatives. The magnitude of a threat will depend on factors such as the morphological and physiological attributes of the prey and its experience, which are often influenced by age and gender. For example, juveniles are presumably less experienced in coping with predators and less familiar with their surroundings than their adult counterparts while adult males may know areas outside their area of primary use better than females do because of their more extensive movements during the mating seasons (Elliott, 1978). For species whose home range is centred on a burrow, distance to burrow should influence magnitude of a threat since it is related to

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familiarity with the surroundings and thus knowledge of availability of refuge (Clarke et al., 1993). The presence of relatives is also likely to be influenced by age, gender and distance to burrow. For example, in promiscuous species exhibiting male-biased juvenile dispersal, adults are more likely than juveniles to have kin as neighbours, since adults may have both offspring and siblings (Burke da Silva et al., 1994). In addition, females are expected to have more relatives in an area near their home range than males do (Shields, 1980).

Although the function of escaping for the prey is very obvious and universal since it usually means avoiding being killed, the function of calling in response to a predator is not. A wide variety of hypotheses has been proposed. Principal functions are that calls benefit the caller through effects on conspecifics such as warning of relatives (Hamilton, 1964) or gathering a group to attack a predator (Hamilton, 1971). Alternatively, calls may be directed at the predator, for example, informing it that the prey is aware of its presence and likely to escape (Zahavi, 1977). Finally, calls may be directed at predators of the predator (Nicolai, 1973 (as cited by Curio, 1978)) that may disrupt the predation sequence (see Table 1). Unfortunately, it is difficult to test hypotheses concerning function of antipredator calls directly. Most tests involve examining predictions concerning contextual, demographic and acoustical correlates of the call. In addition, knowledge of effects on recipients are often crucial.

One of the most widely studied groups in terms of antipredator behaviour is rodents of the family Sciuridae. Several studies have investigated escape behaviour. Some have been mainly concerned with the distance at which the prey initiates its flight from the predator (Dill & Houtman, 1989; Bonenfant & Kramer. in press), some have studied running velocity (Djawdan & Garland, 1988; Trombulak, 1989; Blumstein, 1992), some have been interested in the effect of site familiarity on the escape behaviour and the choice of refuge of fleeing animals (Clarke et al., 1993) and some have focussed on differences in escape responses of prey to different predators (Müller-Schwarze & Müller-Schwarze, 1970; Turner, 1973; Robinson, 1980; MacWhirter, 1992). In addition, a few broader studies about antipredator behaviours have described general aspects of the escape responses of sciurids (e.g. Noyes & Holmes, 1979; Schwagmeyer, 1980; Sherman, 1985).

A number of studies on antipredator calls of sciurids have also been carried out. Some have focussed on the identification of structural components of these calls (Brand, 1976; Melchior, 1971; Koeppl, 1978). Others have demonstrated the predator specificity of these calls (Robinson, 1980; Davis, 1984; Slobodchikoff et al., 1991; Boero, 1992). In addition, some have also investigated the influence of those calls on conspecifics (Schwagmeyer & Brown, 1981; Harris et al., 1983; Weary & Kramer, 1995) and, perhaps more importantly, some have focussed on testing hypotheses concerning their functions (e.g. Sherman, 1977; Dunford, 1977; Loughry & McDonough, 1988; MacWhirter, 1992).

A number of functions have been suggested for antipredator calls of sciurids. For example, it was proposed that Belding's ground squirrels (*Spermophilus beldingi*) "selfishly" manipulate other

squirrels in the vicinity by inducing them to run, thus distracting the predator from the caller (Sherman, 1985). Dunford (1977) and Sherman (1977) were the first to suggest that ground squirrels call in order to warn their offspring or other kin of the presence of a predator. Since then, a great number of studies on sciurids have concluded that certain calls are nepotistic (for example, Leger & Owings, 1978; Schwagmeyer, 1980; Davis, 1984; MacWhirter, 1992). There is some anecdotal evidence that the function of some repetitive sciurid calls is "tonic communication" maintaining vigilance in neighbours and thus warning the caller of the predator's return (e.g., Smith et al., 1977; Lickley, 1984; Loughry & McDonough, 1988). Burke da Silva (1994) suggested that the trill calls of the latter species may inform other individuals about the caller's safety or location, based on differences in calling probability between individuals using holes and those using trees as a refuge. Finally, Owings & Coss (1977) and Burke da Silva (1994) proposed, some calls of California respectively, that ground squirrels (Spermophilus beecheyi) and of eastern chipmunks. (Tamias striatus) could function to vocally mob predators. While mobbing, animals typically assemble around predators, frequently change locations, perform stereotyped wing and/or tail movements, emit loud calls and may attack predators (Curio, 1978). Although, the calling sciurids observed did not perform all of these behaviours, their continual vocalizations and their orientations toward the predator suggest that their calls may be a form of mobbing. This vocal mobbing is thought to deter the predator from hunting in the area.

Despite this start, many uncertainties still exist concerning the adaptive significance of alarm vocalizations in sciurids. It is possible that a given call serves multiple functions. Similar calls might serve different functions for different species. Many researchers have inferred functions from behavioural observation. Of course, such inferences must be made with care since the predictions made to test the hypotheses depends on a number of assumptions and since the predictions often overlap between hypotheses (see Table 1). In addition, natural prey-predator encounters are rare and difficult to observe, experimental predation studies are limited by ethical considerations and simulated attacks are difficult to stage.

Escape and vocal responses have been shown to be influenced by age, gender and distance to burrow in a number of sciurid species. For example, age was correlated with choice of refuge of eastern chipmunks at a distance of 100 m from their burrows (Clarke et al., 1993) and Burke da Silva (1994) observed that male and female juveniles called less frequently than their adult counterparts. Furthermore, gender has been found to influence the propensity to produce antipredator calls in the majority of ground squirrels (e.g Barash, 1975; Sherman, 1977; Dunford, 1977; Leger & Owings, 1978; Schwagmeyer, 1980; Davis, 1984). Moreover, distance to burrow was shown to correlate with distance travelled to reach a refuge, the type of refuge attained (Clarke et al., 1993), and the probability of producing antipredator calls (Sherman, 1985; Burke da Silva, 1994). Similarly, Davis (1984) found that recently immigrated juvenile male

Richardson's ground squirrels (Spermophilus richardsonii) never called whereas non-dispersing juveniles did.

In eastern chipmunks, antipredator responses to terrestrial predators have been studied, but there has been little attention to responses to aerial predators. Escape behaviour and choice of refuge when pursued by human predators in relation to site familiarity was studied by Clarke et al. (1993). Burke da Silva et al. (1994) identified three antipredator calls used by the chipmunks. Trills were described as multi-note calls containing 6 to 11 different downward sloping notes (of 0.8 to 7.3 kHz) given only once by animals fleeing aerial and terrestrial predators just before they reached a refuge. Chips consisted of a series of identical high frequency notes (2.8 to 9.6 kHz) with a rapid downward frequency slope produced in the presence of terrestrial predators. Chucks consisted of a series of identical lower frequency notes (0.4 to 2.5 kHz) also with a downward slope and given in the presence of an avian predator. Burke da Silva (1994) studied the functional significance of chipping and trilling. She eliminated many of the possible hypotheses based on the results of staged encounters with terrestrial predators. Finally, based on location of callers, acoustic characteristics of the call, observations of the predator's behaviour and the correlation between burrow location and the propensity to call, she proposed that the function of chipping was to deter the predator from hunting in the area by mobbing it vocally. She observed age and gender differences in the probability of trilling at 10 m from the burrow suggesting a kin related function, but the occurrence of trills in different seasons and

their performance by juvenile females lead to the rejection of a purely parental function. Based on the context of calling and the behaviour of the caller and other conspecifics. she proposed that trilling did not fit well any of the previously proposed functions but could serve to inform nearby conspecifics that the caller has survived an attack and is about to enter a refuge.

My study was intended to complement that of Burke da Silva (1994). Its main purposes were 1) to describe the antipredator behaviour of eastern chipmunks in response to an aerial predator attack and to test the effects of age, gender and distance to burrow on this behaviour, 2) to obtain an improved acoustical description of the two antipredator calls given in the presence of aerial predators and to describe the extent of variation in acoustical parameters of these calls in the adult population, and 3) to investigate the adaptive significance of these two antipredator calls. In order to meet these objectives, aerial predator attacks were simulated using a live raptor, and the responses of animals of known age category, gender and burrow location were examined.

Chipmunks are ideal test subjects for examining antipredator behaviour since they are small (about 100 g), diurnal and primarily terrestrial. They are monomorphic, relatively non-social and can easily be recognized individually by their great fidelity to a burrow system which they occupy solitarily except during mating and when females are caring for young (Elliott, 1978). Like many mammals, chipmunks have a male-biased dispersal system (Loew, 1992). Both female and male chipmunks mate multiply but females tend to remain near their burrow while males may wander long distances (Elliott, 1978; Loew, 1992; Burke da Silva, 1994). The burrow is usually in the middle of a roughly circular area of primary use extending on average 15 to 25 m from the burrow (Mares et al., 1976; Elliott, 1978; Getty, 1981).

Materials and Methods

Study area, study species and materials

Marking of the chipmunks and preliminary studies were done from July 2 to August 29, 1994, while experimental trials were performed between September 1 and October 16, 1994. The studies were carried out at the McGill University Research Reserve at Mont St. Hilaire, Quebec, Canada (lat. 45° 33' N, long. 73° 10' W). The study area was adjacent to Lac Hertel in the public side of the reserve. It consisted of approximately 40-ha of a beech-maple forest (see Maycock, 1961, for further description of the site). This area shelters a relatively dense population of chipmunks (about 30 individuals per ha (Burke da Silva, 1994)) accustomed to human presence; they did not usually produce any antipredator calls at our approach nor did they stay alert while we remained in the area. On the other hand, they do adopt antipredator behaviour toward a number of terrestrial (raccoons (Procyon lotor), foxes (Vulpes vulpes) and weasels (Mustela erminea)) and aerial ((hawks (Accipiter spp.) and owls (Strigidae)) predator species present in the area.

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For easy individual recognition in the field, chipmunks were using Longworth traps baited with sunflower first captured (Helianthus sp.) seeds. Once caught, an animal was anaesthetized by placing it in a plastic bag which contained a few drops of halothane on absorbent cotton for a few seconds, and examined to determine its gender, weight and age group. Animals were considered juveniles if they weighed less than 90 g. Animals were then marked by clipping their guard hair in unique patterns to reveal their dark undercoat. Animals were released at the location of capture and were kept under surveillance (for a few seconds to half a minute) until they apparently had recovered from the trauma and reached a refuge.

Two one-year old male kestrels (*Falco sparverius*) obtained from the Avian Science and Conservation Centre of the Ma donald Campus of McGill University were used in this experiment. These are small raptors (22-30 cm in length, 51-62 cm in wingspread) of the falcon family, native to and fairly common throughout most of North and South America (Bildstein and Collopy, 1987; Village, 1990). They hunt by hovering or watching for prey from elevated perches. They are very adaptable and opportunistic feeders and will eat almost anything they are able to kill. Although in the wild, kestrels prey mostly and heavily on diurnal small mammals, insects and small birds (Bildstein & Collopy, 1987; Village, 1990), the two trained kestrels used in this study never ate anything but the edible lures (small pieces of dead, newly hatched domestic fowl) which were presented to them on their perches.

The birds were kept in my house or garden (under surveillance) tied with bracelets (small rings of leather held by eyelet-holes), jesses (small leather straps knotted at one end and with a hole at the other one) and leashes (small thread tied to a snap-hook) to their perches (see Fig. 1 a)). In the house, a bowl of water was placed near their perch so that the birds could clean themselves, and newspapers covered the floor. The newspapers and water were changed daily. About once a week, the perches and the whole area used by the birds were thoroughly cleaned. In order to keep the weights of the kestrels nearly constant at a level at which they were willing to fly for food, the birds were weighed and fed between 1/2 and 1 1/2 newly hatched fowls (provided by the Avian Centre and kept frozen until a few hours before use) each day. This maintained them at about the weight at the time they were obtained from the group housing cage at the Avian Centre. At the beginning of training, weights were often lowered slightly below this weight (about 5% lower) to increase the motivation of the birds to obtain food. The training period of one of the birds started on May 27 and on June 13 for the other one and ended with the start of the experimental trials, although they were ready earlier.

To carry out their role as apparent chipmunk predators in the field, kestrels were trained to fly from one perch to another in a straight line; they were placed on a perch and offered a piece of fowl on another one (or on the hand of the handler). As the training progressed, the distance between the two perches was gradually increased to reach about 20 meters. To prevent the birds from flying away when they were outside, they were tied to a fishing line running the whole distance. With further experience, the birds performed similar exercises but in areas with increasing levels of surrounding vegetation and from a starting perch inside a cardboard box.

At this point in the training, the birds were ready to perform exercises very similar to what was expected of them during the staged attack performed in the field; they were now able to fly from a modified cardboard box (51 X 31 X 32 cm) to a perch about 25 cm above ground located about 15 m away. The cardboard box was modifed to accomodate the birds and the experimental procedure: it had small holes on the side for carrying and long ones on top to allow air and light to penetrate, contained a perch and had a sliding door tied to a fishing line so that it could be opened from a distance. This box was attached to a step-ladder at a height of 1.43 m. To prevent the escape of the birds and to standardize their flight path, a fishing line was tied to the box and to the ground perch prior to a trial. On this line, a small ring tied to a cable 30 cm long could move freely. The cable was itself attached to the jesses of the birds. For a better understanding of this set-up refer to Fig. 1b. The modified cardboard box and a similar one were also used to transport the kestrels in a car to the field and to hold them in the field or in a well ventilated car parked in the shade and checked periodically.

Field procedure (staged hawk encounters)

Before a trial, the observer or her assistant spread some sunflower seeds in potential experimental sites and waited for chipmunks to approach. Selected sites were relatively free of low vegetation so that the birds could fly without the lines getting caught. The observer selected the first marked chipmunk to begin hoarding seeds from the patch as the test subject. If this first animal had been tested previously or if it was from an age, gender or distance to burrow category that had been frequently recorded, the next animal coming to the patch was selected as the test subject. The observer or her assistants then found the test subject's burrow entrance by following it from a distance as it made hoarding trips. They then installed the equipment necessary for the trial (see Fig. 1b); 1) the box containing the kestrel was attached to the step-ladder, 2) the ground perch was placed 15.7± 0.3 m (mean ± SE, range: 12.80 -21.70 m) in front of the step-ladder (between 0.75 m and 1.25 m beyond the patch of sunflower seeds), and finally, 3) the fishing lines used to guide the bird's flight path and to open the sliding door on the box were unwound and tied near the ground perch. If chipmunks other than the test subject came to the patch of seeds, other patches of seeds were placed near their burrows to lure them away, or the trial was only started when these animals were not near the experimental patch.

While installing this equipment and waiting for the test animal to perform at least one undisturbed hoarding trip, the observer noted the presence and duration of chipmunk and other animal calls and

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other sounds that could indicate the presence of interfering animals in the vicinity. If antipredator calls were heard, the observer waited about 5 minutes after they had stopped before starting a trial. On the next trip, when the test subject started collecting seeds, she signalled a helper to start a tape recorder, if there were no interfering animals or sounds. She then slowly and inconspicuously opened the bird's box and allowed the bird to fly to the lower perch. Once the sliding door was opened, the kestrel typically flew toward the lure placed on the ground perch within a few seconds. Its flight was silent and its path was usually directed straight toward the focal animal at heights of 1-2 meter above the ground. It then landed on the ground perch. grabbed the lure and proceeded to eat it. Once finished, the bird typically remained more or less motionless for the rest of the trial but sometimes it would flap its wings for a few seconds or move to reposition itself. Except in one case where the kestrel, after eating its lure, flew toward a chipmunk during a preliminary trial, the kestrels never showed much interest in the chipmunks.

The observer started a stopwatch as soon as the chipmunk responded to the apparent attack of the bird by trilling or running. The time of occurrence from the start of the trial of each new behaviour or event was recorded in a notebook. In particular, the observer noted whether the animal did or did not trill, whether it trilled as it started running or when it was already running, the type of refuge used (trees, holes, along log, etc.) and the chipmunk's posture and orientation. The observer continued recording until the animal started foraging again, left the area, or after at least 5 minutes had elapsed following the last vocalization with no evident change in behaviour. When the trial was over, the observer and her assistant measured key distances (e.g., the distance to the burrow from the initial position of the chipmunk, the distance run by the chipmunk to reach a refuge) and the heights above ground level of the perches occupied by the chipmunks during the trial. In addition, the observer noted the date, time, where trials were run, habitat characteristics and any special environmental conditions (e.g., weather, light level). A complete list of the trial variables recorded in the field is provided in Table 2 and the behavioural variables calculated from these are given in Table 3.

To avoid disturbing the chipmunks during a trial, the bird was left on its perch for its whole duration. Because preliminary trials suggested that chipmunks could become habituated to the kestrels, four precautions were taken. First, as soon as the trial was over the bird was carried back to its box and hidden from view. Second, when a trial was over, the observer moved to a distant part of the study area before repeating the procedure so that two consecutive trials were never performed in the same area. Third, at least 30 min were allowed to elapse between the end of one trial and the start of the next. Fourth, no more than eight trials (and on average four) were performed on a given day (usually over an 8 hour period).

If the kestrel failed to fly within 20 s after opening the door, the box was re-closed and a new trial was performed on the next suitable foraging trip. If the kestrel failed to reach the perch because the line attached to the bird got caught on a branch, if the kestrel tried to get away during the trial or if the trial was interrupted because of people approaching, data were included only up to the time of the problem.

A total of 53 successful trials were performed on different individuals. Of these individuals, 43 were adults (22 males and 21 females) and 10 were juveniles (4 males and 6 females). The distances from burrow ranged from 1.5 to 53.2 m (median = 13.5 m, mean \pm SE =17.3 \pm 1.7 m). They were grouped into three distance classes: 1) <15.0 m (n=31), 2) 15.0 - 29.9 m (n=15) and 3) >29.9 m (n=7). These distance divisions were chosen to reflect divisions in the typical use of space by chipmunks.

Acoustical analyses

A Marantz PMD 221 cassette recorder with a Sennheiser MD211 microphone mounted in a Dan Gibson parabolic reflector was used to record vocalizations of tested chipmunks. The frequency response of this system is flat $(\pm 3 \text{ dB})$ over the range of frequencies observed in our calls. The reflector was always well within 5 m of the calling animal except in a few instances where the animal moved before the end of a trial to leave the area. An assistant started the tape recorder a few seconds before the beginning of a trial and stopped it 15 min later. Since the help of an assistant was not always available, the calling responses of only 41 different test subjects were recorded. Of those individuals recorded, 16 were adult males, 17 were adult females, 3 were juvenile males and 5 were juvenile females. For adults of both genders, 7 of the best trills and 10 of the best chucking

bout recordings were used for acoustical analysis. Recordings not used included those in which the calls were too faint or background noise too loud and those in which more than one animal called simultaneously making it impossible to unambiguously distinguish individuals.

Sonagrams (representations of frequency vs. time) and waveforms (representations of amplitude vs. time) were produced using Canary 1.1 on a Macintosh LCIII. This system digitizes calls at 8 bits and uses a sampling frequency of 22.3 kHz. Acoustical measurements were made from these sound representations using the same program by selecting the area of interest (a call, a note or a component of a call). This selection was made by highlighting all the region encompassed by the area of interest up to its most extreme points (beginning and end of the call on the x axis and lowest and highest frequency on the y axis). The program then made the measurements for the selected region of all the acoustical variables studied. For the trill (which constits of a variable number of different notes), a note was defined as a sound producing a continuous trace on the sonagram whereas a call was defined as the entire sequence of notes. For the chuck (which occurred in long bouts of repeated notes, each note often composed of two components), a component was defined as a sound producing a continuous trace on the sonagram, a note was defined as the region that included all the different components present (1 or 2) and chucking was defined as the production of a series of these notes.

For the acoustical analyses of trills, measurements of the acoustical variables (see Table 4), such as duration, minimum and maximum frequencies, were then made for the call as a whole and for each individual note. For each of the variables, the measurement made of the entire call and the mean of the measurements made on its notes were then used as individual values to calculate means and standard error for each gender. In addition, for each of the calls, notes were selected according to their position in the sequence (first and last), their duration (shortest and longest) or their frequency (lowest minimum and highest maximum frequency) and means of these 6 classes of notes were then obtained for each gender.

For the acoustical analyses of the chucks, the selected recordings were sampled 10 times at regular intervals obtained by dividing the time spent chucking into ten equal sections. Sonagrams and waveforms of the first three notes of each section were then produced. From these, all the acoustical variables of interest (see Table 4) were measured for each component of the three notes of a sample and then averaged. These means were then used to calculate means and standard deviations for each individual and each gender and to determine the effect of position in the sequence.

Statistical analyses

All the analyses were performed using Systat 5.2.1. for the Macintosh and an alpha level of 0.05 was considered statistically significant. The order of the trials (as an indication of seasonal progression) had no significant effect on any of the important variables studied (including latency to start chucking, chucking duration of first bout, total chucking duration, distance to the burrow, distance run to reach a refuge, distance to the bird during the first chucking bout, chucking rates and time spent hiding by the animal). Therefore, the data were pooled together irrespective of trial date.

Normality of distribution for each of the continuous variables was first tested with the untransformed data using Kolmogorov-Smirnov goodness-of-fit tests. If the distributions differed from a normal distribution, data were log-transformed and square-root transformed and re-tested for normality. When the untransformed or transformed data did not differ from normal, one-way and two-way ANOVAs were used to test for differences between age, gender and distance to burrow categories, and regression analyses were used to investigate relationships between parameters. If the data could not be transformed to satisfy the assumptions of parametric tests, nonparametric alternatives (such as Kruskal-Wallis and Mann-Whitney U tests) were used. Pearson chi squares were used to test whether categorical variables differed in frequency between age, gender and distance classes. To test differences between related parameters (such as chucking rate between sections of the same bout or acoustical similarities between notes of the same call), paired t-tests (for normal distributions) or Wilcoxon matched-pairs signed-ranks test (when data could not be normalized) were used.

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Results

Response to apparent attack

At the start of the kestrel's flight, chipmunks typically trilled and ran to a nearby refuge and only stopped after reaching it. Shortly after disappearing into the refuge, they emerged and started chucking. Usually chucking continued for many minutes, but gaps sometimes separated the first few chucks from the start of a continuous bout or divided the chucking period into a series of bouts. Chucking animals were almost always in a stationary, alert posture, on a raised perch such as a stump or a rock, and facing the predator. Occasionally, they changed position or groomed during the chucking period. After they stopped chucking, chipmunks typically remained quiet for a short time then returned to foraging or left the area. In some trials, nearby chipmunks other than the focal animal also began chucking. The following sections quantify these patterns and examine how variation is related to gender, age and distance from the burrow. The patterns are summarized by age and gender in Table 5 and by distance to burrow categories in Table 6.

All chipmunks exposed to the simulated aerial attack made a rapid (1 - 2 s) and usually straight run to a nearby refuge. None remained motionless, continued to run for long distances or moved from refuge to refuge. Distances run ranged from 0.1 to 10.8 m, but half the individuals ran less than 2.7 m and the great majority less than 5 m. Distance run was not significantly influenced by age, gender or distance from burrow. The refuges used included 1) the

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subject's burrow. 2) other holes in the ground. 3) structures with overhead cover that allowed the animal to be partially or completely hidden (e.g., bushes, brush piles, holes or cracks at the base of trees and rocks), 4) positions near vertical structures that provided side protection but little or no overhead cover (e.g., the bases of trees, rocks, logs and fallen branches) and 5) fallen leaves. None of the chipmunks climbed up trees. The proportion of animals using these five types of refuge varied with age/gender category and distance to burrow (Table 5 and 6). For analysis, burrows, holes and overhead cover were grouped into a high protection category, side protection positions were considered as a low protection category, and the three individuals that used leaf litter were excluded. Refuge choice was affected by age category with juveniles being more likely to seek high protection and adults most often seeking low protection. This effect was significant using all observations combined ($\chi^2 = 8.624$, df = 1, p < 0.004). When only individuals less than 15 m from their burrow were considered because few juveniles were tested in other distance categories, the difference between adults and juveniles remained significant ($\chi^2 = 6.751$, df = 1, p < 0.01). Gender and distance to burrow had no effect on choice of refuge.

Over 90% of the chipmunks (48 of 53) gave a trill during their initial flight from the predator. Over 90% of these trills (44 of 48) were early trills (i.e. given at the beginning of the flight). The small number of individuals that trilled late in the flight or did not trill at all makes it impossible to test whether there were effects of age, gender and distance to burrow on these probabilities. Hiding time formed a highly skewed distribution, with some animals emerging after a delay of only 2 s and one hiding for more than 16 minutes (median = 6 s, n = 52). There was no indication of any effect of age, gender or distance to the burrow on hiding time. Adult chipmunks using holes hid significantly longer than adults using either other types of overhead or side protection (holes vs side protection: Mann-Whitney U Test, U = 61.00, n₁ = 3, n₂ = 22, p < 0.02, and holes vs overhead protection: U = 38.5, n₁ = 3, n₂ = 14, p < 0.03). Adults with overhead protection other than holes hid significantly longer than those using side protection (U = 222.00, n₁ = 14, n₂ = 22, p < 0.03, Fig. 2). Like adults, juveniles using holes hid significantly longer than those using overhead protection (U = 12.00, n₁ = 2, n₂ = 6, p < 0.05, Fig. 2). Too few juveniles used side protection to permit statistical comparison.

All focal chipmunks chucked during the trial and none chipped except one juvenile that switched from chucking to chipping after an adult came to the area and started to chip (possibly in response to the observer's presence since the simulated attack had long been over and the bird was immobile on its perch). Most individuals began a regular series of repeated chucks starting with the first note. However, 7 of 52 animals gave 1 or 2 notes separated by longer than usual intervals before starting a regular chucking bout. Typically, animals started chucking only after emerging at least partially from their hiding place and while remaining very close to it. However, slightly more than 13% (7 of 52) gave at least some chucks while hiding and about 10% (5 of 52) started their first regular chucking bout without even their head out of their refuge. Although the median interval between emerging and the start of the first chucking bout was zero, some started to chuck more than 6 minutes before emerging while others waited close to 9 minutes after their reappearance before starting to chuck. No significant differences in the interval between emerging and the start of chucking were observed among age, gender and distance to burrow categories.

Like hiding times, chucking latencies from the first reaction to the kestrel were highly skewed, with many animals beginning to chuck after only a short delay and a few waiting more than 6 minutes (median = 10 s). There was no indication of any effect of age, gender or distance to burrow on chucking latency.

Chipmunks spent a considerable but highly variable amount of time chucking. The chucking periods (from the start of the first chucking bout to the last chuck of the trial) had a median length of 13.1 min (range = 7 s - 31.6 min) and were approximately normally distributed. There was no effect of age on chucking period. However, at intermediate distances from their burrow, females chucked longer than males (one way ANOVA, $F_{1,13} = 6.156$, p < 0.04, Fig. 3). Distance to burrow had a marginal effect on adult males (one-way ANOVA, $F_{2,19} = 3.271$, p < 0.07), where animals close to their burrow tended to chuck for a longer period.

Only 40% of the chipmunks chucked without stopping throughout their chucking period (21 of 52). The others stopped once (23%), twice (30%) or three times (6%). There was no effect of order

on pause duration. On the other hand, the duration of the first bout was significantly longer than the second (Wilcoxon signed rank test, Z = -2.479, p < 0.02). There were no significant differences between the first and the third bout or between the second and the third bout. Between chucking bouts, the animals sometimes moved to another location. Otherwise, they continued to face the predator remaining motionless or occasionally groomed.

For most animals, the majority of the period from the start of the first bout until the end of the last bout was actually spent chucking (median = 96.3%, n = 52, Fig. 4). However, some individuals spent less than 30% of the time chucking. Distance to burrow did not appear to influence the percentage of time spent chucking. However, juvenile males spent considerably less time chucking than other categories (juvenile males vs juvenile females : U = 24.00, n₁ = 4, n₂ = 6, p < 0.01; juvenile males vs adult males: U = 76.00, n₁ = 4, n₂ = 21, p < 0.02). There were no correlations between percent time chucking and other characteristics of the response to the kestrel, including hiding time and the length of the chucking period.

Chucking rate varied between individuals and between parts of the chucking period from 0.3 notes/s to nearly 5.9 notes/s. The maximal value was only observed for a short period in one animal. To further look at this variation, chucking rate for about one minute at the beginning (first minute), in the middle (mid-point or as close to it as possible if the mid-point was during a pause) and end (last minute) of the chucking period was examined. Chucking rate at the beginning ranged from 0.3 to 2.8 notes/s (median = 1.4 notes/s). Rate

in the mid-period ranged from 0.5 to 2.8 notes/s (median = 1.5 notes/s). Rate at the end ranged from 0.3 to 2.8 notes/s (median = 1.1 notes/s). There was no significant difference between chucking rate at the beginning and middle of the chucking period, but chucking rate at the end was significantly lower than at the beginning (Wilcoxon signed rank test, Z = -2.117, p < 0.035) and middle (Z= -3.762, p < 0.001). Males chucked at a significantly higher rate than females at the end of the chucking period (F 1, 50 = 7.474, p < 0.01), but there was no difference between genders at the beginning or middle period. Chucking rates were not significantly related to age or distance to burrow.

A variety of disturbances during the chucking period affected vocalizations. Trills were produced 13 times by 11 different individuals during the chucking period. Of the 11 cases produced by the different individuals, 7 were associated with wing flapping by the kestrel, 2 with less intense kestrel movements and 2 with other gusts of wind that moved the vegetation. Trills occurred after about 41% of the wing flaps (7 of 17), 13% of other kestrel movements (2 of 15) and 40% of sudden gusts of wind (2 of 5) that were noted during observations. Moving by the chipmunk was strongly associated with the occurrence of trills. Ten animals both trilled and moved while only 1 trilled but did not move and 4 moved but did not trill following disturbances.

Some disturbances such as kestrel movements and gusts of wind also affected chucking behaviour. The observer noted shortterm reductions in chucking rate immediately following disturbances

on 30 occasions and cessation of chucks for more than 5 s on five other occasions. Of 34 different individuals exposed to a disturbance, chucking rate declined in 18 cases and stopped in four others. Decrease in rate occurred after 64% of the wing flaps of the kestrel (9 out of 14 cases), 53% of its less intense movements (8 of 15) and 20% after sudden gusts of wind (1 of 5). On the other hand, chipmunks stopped chucking after 21% of the wing flaps (3 of 14 cases), 0% of the less intense movements (0 of 15) and 20% after gusts of wind (1 of 5).

Chucking animals were almost always in the stationary alert posture described by Elliott (1978). Usually, the chipmunk kept all four feet on the substrate rather than adopting an upright posture. Sometimes, chipmunks changed chucking location (defined as a place where animals emitted more than 3 notes). Of 52 animals, 45% did not change location, 27% moved once, 25% moved twice and 4% moved three times. None moved more than three times. While moving, they often ceased chucking or modified their chucking rate. Chucking distances varied from 0.8 to 18.3 m from the kestrel. Medians (and ranges) of the distances from the bird for the first, second and third chucking location were 3.4 m (0.8 - 11.1 m), 3.7 m (0.8 - 13.7 m) and 7.7 m (2.6 - 18.3 m), respectively. The differences were statistically significant (first vs second: Z = 3.330, p < 0.001; second vs third: Z = 3.238, p < 0.002: first vs third: Z = 3.237, p < 0.0020.002). No significant differences in distance between chucking location and the kestrel were observed among the various age, gender and distance to burrow categories except that juvenile males

were closer than juvenile females for the first chucking location (Mann-Whitney U test, U = 22, P < 0.04 and $n_1 = 4$ and $n_2 = 6$).

Chipmunks often perched above ground level when chucking. Perches included stumps, rocks, logs and aboveground roots, but no animals called from trees. Perch heights ranged from 0 to 80 cm with medians of 0, 23 and 34 cm for the first, second and third chucking locations, respectively. Perch height increased between the first and second location (Z = 2.706, n = 25, p < 0.007) but not between the second and third. Perch height was not related to age, gender or distance to burrow.

All but 2 of the 51 chipmunks spent most of the duration of their first chucking bout (while visible to the observer) oriented to within 30° of the kestrel. The other two animals spent the majority of their time oriented between 30° and 90° of the kestrel. None of the chipmunks spent most of their first chucking bout oriented away from the predator. The head orientation of only one animal could not be observed during most of its chucking period while some animals were not visible only for short parts of their chucking bout. The median percent time oriented to within 30° of the kestrel during the first chucking bout was 91.5%. Median percent times oriented between 30° and 90° and more than 90° from the kestrel were zero (Fig. 5). This strong orientation toward the predator continued for the rest of the trial. Exceptions occurred mainly when the animal was about to change chucking location, when an unusual noise came from closeby and when the animal was about to initiate a new activity such as foraging.

After they stopped chucking, most chipmunks waited a short time (0 s to 9.5 min, median = 35.5 s) then returned to foraging or left the area. Age, gender and distance to the burrow had no significant relationship with this delay. In addition, no difference in delays were found between animals that returned to foraging and those that left the area. About 16% (8 of 51) of the animals did not return to foraging or leave the area, but remained motionless for at least 5 min. Total response times (from first reaction to the moment it started to either forage or leave the area or had remained more or less motionless for 5 min) varied from 90 s to more than 30 min (median =15.5 min). Total response time and the final activity (forage, leave or remain motionless) did not differ significantly among age, gender and distance to burrow categories. However, response times were longer for those that remained motionless for at least 5 minutes after the end of chucking than for those that foraged (Mann-Whitney U Test, U= 9.00, $n_1 = 8$, $n_2 = 12$, p < 0.003) or left the area $(U = 43.00, n_1 = 8, n_2 = 31, p < 0.005)$.

In 20 of the 53 trials, one chipmunk other than the focal individual produced chucks, and in 4 additional trials, 2 to 4 other chipmunks chucked. In 87.5% of the 24 cases in which non-focal chipmunks chucked, the tested animal was "joined" by these individuals at some time during its chucking period. In the majority of those cases (61.9%, 13 of 21), the non-focal individuals only chucked while the tested animal was itself chucking. The median latency to start chucking (from the initial reaction of the focal animal) by the non-focal individuals was 223 s (range = 6 to 760 s, n

= 23). The median chucking period duration of non-focal individuals was 218.5 s (range = 2 - 1339 s. n = 22). The great majority of these animals were quite close to the observers. in conspicuous locations and within sight of the predator. Only 27.6% of the non-focal individuals heard chucking (8 of 29) could not be visually located by the stationary observers during the trials. Median distance from the observed non-focal chipmunks to the kestrel was 7.5 m (range = 1.1 -16.2 m. n = 17). Only 5 animals were not perched (17.9%) and the median perch height for all the animals was 15 cm (mean = 13.5 cm, range = 0 - 45 cm, n = 17). The presence of another chucking animal was not significantly related to the chucking period duration of the focal animal, its percent chucking time, its total response duration nor its chucking rates at the beginning, middle and end of the chucking period.

Acoustical characteristics of antipredator calls

Trills

Trills are highly variable calls that consist of a short series of rapid notes that are usually high pitched and acoustically variable (Fig. 6, Table 7). They may resemble bird calls to inexperienced listeners. The mean \pm standard error (range) number of notes in the 14 adult calls studied was 8.00 ± 0.97 notes (3 - 13 notes) with a total duration of 545.37 \pm 60.67 ms (97.15 - 1027.32 ms). The mean minimum frequency per call was 2.94 ± 0.29 kHz (1.09 - 4.45 kHz) and the mean maximum frequency was 8.42 ± 0.33 kHz (6.12 - 10.44

kHz). The mean position of the note of peak amplitude was 2.86 - 0.56 (1 - 8). The frequency at the peak amplitude was 5.81 ± 0.27 kHz (5.06 - 8.52 kHz) and occurred 144.92 \pm 39.43 ms (6.94 - 447.56 ms) after the start of the call. There was no significant difference between males and females for any of these parameters. but females tended to have a greater frequency range than males (F = 4.112, df = 12, p < 0.07, (Table 7)).

The fourteen trills contained 112 individual notes. These notes usually had a great variation in frequency (mean \pm SE = 2.71 \pm 0.14 kHz, (0.35 - 6.33 kHz)) in a short time (22.62 \pm 0.90 ms (2.00 - 55.55 ms)), and usually had a downward sweep. The mean interval length between the end of one note and the start of the next was 59.72 \pm 9.308 ms (0.00 - 519.00 ms). The overall mean minimum frequency of notes was 4.24 \pm 0.11 kHz (1.09 - 7.74 kHz) while their mean maximum frequency was 6.95 \pm 0.13 kHz (1.82 - 10.21 kHz). The mean frequency at peak amplitude of notes was 5.74 \pm 0.10 kHz (1.50 to 8.52 kHz). Harmonics were never observed for notes in trills. Often, one or more notes (7 of 14 trills) exhibited a small increase in frequency followed by a decrease (see Fig. 6). There were on average 1.29 \pm 0.44 (0 - 5) of these chevron-shaped notes per call. Their position in the sequence of notes was quite variable (mean position first chevron-shaped note = 3.43 \pm 1.04 (1 - 8)).

The characteristics of the first and last, shortest and longest, and lowest and highest frequency notes of each trill are: given in Table 8. According to paired t-tests, the first notes of trills were significantly longer (t = 2.87, df = 13, p < 0.02), had a significantly
greater frequency range (t = 5.37, df = 13, p < 0.001) and had higher maximum frequency (t = 4.03, df = 13, p < 0.002) and minimum frequency (t = 3.47, df = 13, p < 0.005) than the last notes of the calls (Table 8). No significant differences were observed for frequency of peak amplitude. None of these parameters differed significantly between males and females.

As would be expected, the longest notes of a trill were significantly longer (t = 8.62, df = 13, p < 0.001) than the shortest notes (Table 8). In addition, they had a significantly greater variation in frequency (t = 3.98, df = 13, p < 0.002), a lower minimum frequency (t = 3.23, df = 13, p < 0.007) and they came significantly earlier in the sequence than the shortest notes (t = 2.44, df = 13, p < 0.03). No significant differences were observed between the longest and shortest notes for highest maximum frequency or frequency of peak amplitude. No significant differences were observed between that females had longer longest notes than males did (38.48 ± 3.87 ms vs 27.81 ± 2.04 ms; df = 12, F = 5.95 and p< 0.04).

Not surprisingly, the notes with highest maximum frequency were significantly greater in maximum frequency (t = 4.86, df = 13, p < 0.001), minimum frequency (t = 3.30, df = 13, p < 0.006) and highest peak frequency (t = 2.58, df = 13, p < 0.03) than the notes with the lowest minimum frequency (Table 8). No significant differences were observed in duration, variation in frequency or position in the note sequence between notes with the highest maximum and lowest minimum frequency. In addition, no significant differences were found between males and females for the two types of note except that the lowest frequency notes of females were significantly longer (31.40 \pm 3.87 ms vs 17.51 \pm 2.16 ms; df = 26, F = 9.84 and p < 0.009) and had a greater variation in frequency (4.41 \pm 0.66 vs 2.43 \pm 0.42; df = 26, F = 6.23 and p < 0.03) than those of males.

Regression analyses relating duration, variation in frequency, minimum and maximum frequency, frequency of peak amplitude, intervals between notes and time of peak amplitude to sequence order of notes revealed no significant relationships. Regression analyses also failed to reveal significant relationships between these parameters and the measured distance of the caller to its burrow.

In some trials, it was possible to record more than one trill by the same individual because of disturbances such as wing flapping by the kestrel. In two cases, two good quality recordings were obtained and in three cases three good quality recordings of trills were obtained. Sonagrams revealed tremendous within-individual variation in trill characteristics. These included number of notes, the presence of chevron-shaped notes, the duration of the calls, their variation in frequency, their minimum and maximum frequencies, their frequency at their peak amplitude and the timing of this peak amplitude. No consistent changes were detected in the characteristics of trills in relation to the number of trills given by the same individual.

Chucks

Chucking consists of a series of similar notes, described as similar to the sound of an axe hitting wood or horse's hooves on concrete pavement (Seton, 1929), repeated in bouts lasting from a few seconds to many minutes. Acoustical analyses revealed that chucks often consisted of two different components differing in frequency range, one of which had not been previously described (see Fig. 7). Figure 7c) shows that the new component is not simply a harmonic of the other component. Both the new component and the harmonics of the other can be clearly observed. Eighteen of the 20 different animals recorded had two components in the majority of the 30 notes analyzed. The second component was present in all chucks, but 10% of the chipmunks lacked the first component in the majority of their chucks. The mean percentage of notes with two components per animal was $86.7 \pm 6.3\%$ (0 - 100%). The first component was high pitched with a mean minimum frequency of 4.067 ± 0.103 kHz (2.991 - 4.842 kHz) and mean maximum frequency of 6.099 ± 0.194 kHz (4.694 - 7.515 kHz) and a frequency at its peak amplitude of 5.200 ± 0.134 kHz (4.097 - 6.144 kHz). Its variation in frequency was 2.027 ± 0.192 kHz (0.801 - 3.361 kHz) and it lacked harmonics. Duration was on average 17.30 ± 1.07 ms (8.33 - 25.83 ms). The second component was lower pitched with a mean minimum frequency of 0.958 ± 0.051 kHz (0.666 - 1.777 kHz), a mean maximum frequency of 2.089 ± 0.062 kHz (1.646 - 2.688 kHz), and a frequency at peak amplitude of 1.457 ± 0.038 kHz (1.215 - 1.983 kHz). This component had harmonics 80% of the time. The

3.2

mean number of harmonics was 2.35 ± 0.42 (0 - 5). These harmonics ranged from the first to the sixth multiple of the fundamental frequency. The duration of this component was 21.48 ± 1.51 ms and its variation in frequency was 1.132 ± 0.0747 kHz (0.362 - 1.704 kHz). Usually there was no gap between the first and second components; the two components often partially overlapped in time. The interval between the start of the first component and the start of the second component averaged 0.074 \pm 0.042 ms (0.006 - 0.79 ms).

There were large differences in acoustical characteristics of chucks of different individuals, but a strong consistency within an individual over the course of its chucking period. Some had both components of the chuck while others had only the second component. Some had no harmonics while others had 1 to 5. Some had a higher amplitude in their first component while others in the second one. ANOVAs revealed highly significant differences among duration, variation in frequency, individuals for the variables of peak minimum and maximum frequency, and frequency amplitude (F values ranging from 6.203 to 53.4, df = 19, p < 0.0001). There was no effect of position in the chucking sequence (1 to 10). There was no difference between males and females in the proportion of animals that produced a chuck consisting of the two components, in the delay between components, in the proportion of calls which had harmonics of the second component, or in the frequency measure of each component. Regression analyses revealed no significant relationship between acoustical variables and distance

of the caller to its burrow, time from the start of the chucking period. distance to the kestrel or perch height.

Discussion

Escape behaviour in response to an aerial predator attack

There is considerable evidence that the chipmunks regarded the simulated aerial predator attack by the kestrel as a serious threat. The animals never responded to the slight movement of the observer while opening the box nor to the opening of the door. They only changed their behaviour as the bird was starting its flight. They all adopted escape behaviour: they ceased foraging and ran to refuges very early in the kestrel's flight. All of them also vocalized at some moment during the trial; although not all of the individuals trilled, they all chucked and often did so for more than 15 min. These antipredator behaviours are typical of chipmunks responding to a real predator in natural situations (see Appendix 1). In addition, many chipmunks did not return to the food patch, even after a long delay, despite its high food density compared to the surrounding area. Furthermore, they responded to the perched kestrel as a danger, often trilling, running to a refuge, and lowering their calling rate when the kestrel moved.

Our study and the two experiments of Clarke et al. (1993) suggests that chipmunks have a good knowledge of escape paths and refuge locations when they are within their area of primary use or

when they are voluntarily coming to a patch of food. Irrespective of age, gender and distance away from burrow, the path to a refuge used by a chipmunk escaping the avian predator or the human pursuer was typically very straight and the distance travelled was usually very short. Clarke et al. (1993) observed that chipmunks released 100 m from their burrow travelled about twice as far to reach a refuge as did animals released 10 m from their burrow. Possibly because of a small sample size at distances greater than 30 m (n = 7) and no cases approaching 100 m, such a distance effect was not observed in the present study. It is surprising that distance to reach a refuge is not more influenced by distance to burrow and is not significantly influenced by age and gender. One might have expected older individuals, those closer to their burrow and possibly males which wander more during mating seasons to know the locations of more refuges and therefore to have a shorter distance to run. A knowledge of escape paths and refuge locations may be a prerequisite for a chipmunk to come foraging in an area or that information might be gained very rapidly as the animal makes exploration and foraging trips (note that animals were allowed to make a few trips before a trial began). An alternative explanation could be that chipmunks simply locate a refuge as they are fleeing. The great variation in refuge type attained may imply that chipmunks are not very selective and simply take cover in the nearest suitable location. However, in two cases where the same individual was observed to react to both a wild raptor and the simula...d attack during a single observation period, the animals hid 2 in the identical place both times (see Appendix 1). Finally, different animals tested at the same site often chose the same refuge even though their initial position was different. This suggests that the choice of refuge is not random and that chipmunks might indeed depend on a knowledge of specific refuge locations.

Although chipmunks escaping the simulated kestrel attack never chose to climb trees, there were great variations in the type of refuge used. They often hid in refuges offering a high level of protection such as holes in the ground other than their burrow, cracks in stumps, in bushes etc. Surprisingly, they also often hid in shelters offering no overhead protection such as along logs or fallen branches. Perhaps, the best escape response to an aerial predator is to get close to a solid object no matter what type, as quickly as possible. Raptors typically attack by a single swoop, rely on surprise to catch their prey and often do not attempt to hunt after the prey has noticed their presence (Morse, 1973; MacDonald & Henderson, 1977; Leger et al., 1980; Pettifor, 1990; but see Temple 1987). Chipmunks escaping a first attack and hiding near any structure that prevents the bird from catching them in a direct swoop might be safe. In addition to providing sufficent safety, structures providing side protection only probably allow the escaping animal to easily keep track of the predator's movements. A high propensity to monitor the predator has been reported in a number of sciurids. For example, numerous species of marmots stop before entering their burrows, visually follow the predator and use promontories so as to maintain visual contact (e.g. hoary marmots, Marmota caligata (Noyes

& Holmes, 1979), Belding's ground squirrels (Robinson, 1980, 1981), woodchuck, Marmota monax (Bonenfant & Kramer, in press)).

Refuge choice was influenced by age class, with juveniles being more likely to use refuges providing high protection and adults those with lower protection. Because adults are likely to have had more time to discover refuges, it seems they would more likely know the availability of high quality refuges than juveniles would. Therefore, the choice of safer refuges by juveniles is unlikely to be a result of better knowledge of available refuges. Perhaps more experience with predators makes adults less vulnerable and more likely to favor predator monitoring in a trade-off between gaining more information and greater safety.

Only 2 of 53 individuals hid in their burrow even though 17 of them were within 10 m and six were within 5 m of their burrow. This propensity for chipmunks not to use their burrow as a refuge was also observed in studies using a human pursuer (Clarke et al., 1993). This behaviour is contrary to the behaviour of most other ground-dwelling sciurids which do use their burrow when confronted with a predator (e.g., Belding's ground squirrels (Robinson, 1980, 1981); black-tailed prairie dog, *Cynomys ludovicianus* (King, 1955); woodchuck (Schoonmaker, 1966)). Clarke et al. (1993) suggested that chipmunks may attempt to conceal their burrow location from predators because they often travelled a greater distance to reach a refuge than the distance initially separating them from their burrow. They also noted the contrast between the cryptic burrow entrances of chipmunks and the obvious mounds of earth at the entrance to burrows of ground squirrels (Spermophilus sp.), prairie dogs (Cynomys sp.) and marmots (Marmota sp.). Contrary to what was observed with a human pursuer, chipmunks escaping an aerial predator never used refuges farther than their burrow entrance (except one individual which covered 1 m more). Choice of refuge for chipmunks avoiding an aerial predator might therefore be based on proximity to the refuge rather than avoidance of burrow.

Further comparisons of this study's results with those of Clarke et al. (1993) reveal other differences in escape responses of chipmunks to terrestrial and aerial predators. For example, contrary to our findings about refuges sought by chipmunks escaping an aerial predator, Clarke et al. (1993) observed that the choice of refuge of chipmunks being chased by a human was limited and influenced by distance to burrow. Animals within 10 m of their burrow typically chose to hide in holes in the ground but they usually climbed trees when at distance of 100 m. The differences in chipmunk responses to aerial and terrestrial attacks observed in the two studies could be due to the differences in experimental set-ups; a single attack by the kestrel oriented toward the initial position of a chipmunk vs a pursuit by a human of a test subject. For example, chipmunks might have eventually reached holes in the ground if they had been pursued by the bird. On the other hand, these differences could also be the result of differences in antipredator tactics. Given what is known about hunting behaviours of aerial and terrestrial predators, the different escape strategies of chipmunks seemed appropriate responses to the hunting behaviour of these two types of predator.

When an aerial predator or another fast moving predator is detected, time is usually not available to ascertain its exact intentions. Therefore the most suitable evasive action is probably to run immediately to the nearest suitable refuge. On the other hand, the threat from a terrestrial predator is less immediate since they are usually slower. Therefore, there is more time to decide on the proper refuge and a greater distance can be travelled to reach it. Selection of the closest refuge available in response to an aerial predator has been observed in other terrestrial sciurids (e.g. Turner, 1973; Sherman, 1985; MacWhirter, 1992). Moreover, some of these authors have observed that these same animals were more selective in choice facing terrestrial of refuge when predators (Turner, 1973: MacWhirter, 1992).

Although some animals hid for considerable time, most of the chipmunks disappeared from view only for a few seconds. Short hiding times might be a result of an advantage to monitoring the predator. Hiding time was not significantly influenced by age, gender and distance to burrow but was correlated with refuge chosen. Adults using holes hid for longer periods than those using other types of overhead protection which in turn remained hiding longer than those using side protection refuges. Juveniles in holes hid for longer periods than those using overhead protection refuges. Differences in hiding time could result from individual differences in wariness; more wary individuals would select safer refuges and hide longer. It could also be a result of differences in the propensity to monitor the predator; animals with a higher propensity to monitor the predator would possibly reach side protection refuges because they allow prompt monitoring of the predator. Conversely, the difference in hiding time might be a result of differences in ability to monitor the predator from different refuge types. Animals in holes or with overhead protection refuges would lose sight of the predator making early emergence risky because of the possibility of a new attack. Animals hiding near side protection would rapidly determine whether the predator was nearby and thus be more secure about reappearing.

Vocal behaviour in response to an antipredator attack

Trill

The first antipredator call given by chipmunks in response to the simulated attack of the kestrel was the trill. It is a nonrepetitive, moderately loud call which consists of several acoustically different notes produced in a rapid sequence. A number of authors (Seton, 1929; Allen, 1938; Damon, 1941; Wolfe, 1966 (as cited by Yahner, 1978); Dunford, 1970; Yahner, 1978; Burke da Silva et al. 1994) have described the trill of chipmunks more or less similarly but most of them used the name chip-trill to refer to it. Because chipmunks do emit a similar but longer call during agonistic interactions with conspecifics, Burke da Silva et al. (1994) following Elliott (1978) suggested that the name chip-trill be reserved for agonistic calls and trill for calls produced while escaping. Our study of 14 trills given by different individuals in response to the kestrel and by limited evidence provided by animals for which trills were recorded more than once reveals that the exact sequence of notes is unique from call to call. The number of notes, the duration of the call, and its extreme frequencies are extremely variable between calls. In addition, there is considerable variation within a call in the duration of the notes, their extreme frequencies and the time interval between them (see Table 7 and 8). Consequently, tremendous differences exist between calls. Neither of the two chip-trills presented by Dunford (1970; Fig. 7 B and C) or the two trills illustrated by Burke da Silva et al. (1994; Fig. I e and f) exactly resemble the trills observed in this study but they are within the range of observed variation. Similar mean note number and mean minimum frequency to those observed in this study were reported by Burke da Silva et al. (1994), but they observed lower mean intervals between notes, mean call durations and mean maximum frequencies. They also observed a lower range in note number, interval between notes and duration of call. This is not surprising since they had a smaller sample size (6 vs. 14). Since neither Dunford (1970) nor Burke da Silva et al. (1994) clearly reported whether their recorded trills were produced in response to an aerial or a terrestrial predator, it is possible that some of the variation between calls of the different studies can be explained by subtle differences in trills given to different predators. Further studies are needed to investigate this possiblility.

A call similar to the trill of eastern chipmunks has been described in western chipmunks (formerly classified in the genus *Eutamias*) under the name chippering by Brand (1976), whereas the

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trill he described is a variation in temporal patterning of chipping. Various other sciurid species emit calls which are somewhat acoustically similar to trills but are given in a different context. They are produced in response to the sighting of terrestrial predators. Examples include the round-tailed ground squirrel. *Spermophilus tereticaudus* (Dunford, 1977), the thirteen-lined ground squirrel (Motacha, 1977; Schwagmeyer & Brown, 1981) and Belding's ground squirrel (Robinson, 1980; Leger et al., 1984; Sherman, 1985).

Trills in eastern chipmunks are produced in strong and sudden alarm situations. Chipmunks exposed to predator attacks usually trill simultaneously as they start to run or while running to a refuge. Although trills are produced in response to both terrestrial and aerial predators, the exact context of trill production may differ between predator types. Burke da Silva's (1994) study of animals trilling in response to pursuit by a human lead her to conclude that fleeing animals tended to trill upon reaching a refuge, whereas in the present study chipmunks tended to call early in flight. This difference might arise because animals fleeing an avian predator might select a closer refuge than those fleeing a terrestrial predator so that they are about to reach a refuge even as they start running. However, in the present study, animals that trilled later did not seem to run farther. The difference in time of trilling could also be due to a difference in the type of refuge used. Burke da Silva (1994) found that animals using holes were more likely to trill than those using trees as refuges. In this study, chipmunks did not use trees, but most animals did trill despite using a wide range of other refuges. Another

possibility is that the apparent avian attack was a much stronger stimulus than pursuit by a human which could influence the timing of the trill. Finally, differences in timing of the trill might be a reflection of different antipredator strategies. Indeed, timing of a call in reponse to aerial and terrestrial predators has been shown to vary with predator type in other sciurids. Similar to chipmunks, Belding's ground squirrels vocalize in response to an aerial predator while running to safety but call to a terrestrial predator after reaching a vantage point (Sherman. 1985). By contrast, Columbian ground columbianus. squirrels, Spermophilus typically produced a nonrepetitive call before running when exposed to a badger model and while running or after reaching a burrow when exposed to a flying disk (MacWhirter, 1992).

Calls strongly associated with escape behaviour have not been very well described in other sciurids. The churr call of the Columbian ground squirrel is probably the most similar to the trill in context. It is produced just before entering the burrow and consists of a fading series of "shrill chirps" given in a rapid succession (Betts, 1976; Harris et al., 1983). On the other hand, calls usually associated with alert behaviours when a terrestrial predator is sighted are also often given by sciurids as they run to a refuge (e.g. Sherman, 1985).

The great majority of chipmunks exposed to the staged kestrel attack trilled, and no differences in the probability of trilling were observed between individuals of each age, gender and distance to burrow category. In contrast, Burke da Silva (1994) using a human pursuer found difference in the probability of trilling between categories and between chipmunks reaching different refuge types. The probability of trilling observed in this study (over 90%) was higher than that observed using a model aerial predator (78%, Burke da Silva et al., 1994) or using a human pursuer (less than 80%, Burke da Silva. 1994). Thus the difference in trilling among categories may be an effect of lower apparent threat. Perhaps a strong threat induces a larger percentage of animals to call, obscuring differences among age, gender and distance classes. Observations of two natural encounters are in favor of this hypothesis (Appendix 1) because the chipmunks did not trill when the predator was relatively far and not directly threatening. In addition, a number of studies have found an effect of size, form, speed, species and distance away from a predatory stimulus on the probability of calling in sciurids (e.g. Owings & Virginia, 1978; Robinson, 1980; Slobodchikoff et al., 1991) and other animals (e.g. Klump & Curio, 1983; Alatalo & Helle, 1990; Evans, et al., 1993).

Functions of the trill

It is very hard to reject with complete certainty possible functional explanations of antipredator calls because observations may be in agreement with some predictions of a function while not with others and since the predictions often overlap between hypotheses. Nevertheless, a number of the previously proposed functions of antipredator calls can be ruled out as explanations of trill production in chipmunks because observations seem to directly contradict the predictions (see Table 1). First, five hypotheses can be rejected on the basis of the context of call production. Since trills are given only once while chipmunks are fleeing a pursuit by a predator or when the predator appears to be about to pursue them and not simply when the predator arrives or remains in the area, hypotheses #1 (attract), #3 (warn), #4 (maintain vigilance), #7 (sentinel), #11 (mob), #12 (invite pursuit) and #13 (defence) can be excluded. Second, some functions of trilling can be refuted based on identity of the calling chipmunks. Since the great majority of the chipmunks exposed to the simulated aerial attack by the kestrel trilled irrespective of age, gender and distance to the burrow categories, it seems that trilling in response to an aerial predator confers a universal benefit to the caller and rules out that the call serves only a nepotistic function (#3 (warn), #5 (teach), #7 (sentinel) and #10 (distract)). Otherwise animals less likely to have relatives in the area of the attack such as juveniles, males and animals farther away from their burrow should have a lower probability of calling. Third, can be rejected on the basis of the acoustical hypotheses characteristics of the trill itself. Indeed, hypotheses #4 (maintain vigilance), #7 (sentinel), #11 (mobbing), #13 (defence), #14 and #15 (to attract predators or competitors of the predator) can be dismissed since trill involves only a few notes that do not resemble any threatening predator calls, is not repetitive and is not given particularly loudly. Finally, some hypotheses can apparently be ruled out based on the behaviour of call receivers. Since animals were never observed assembling into groups or fleeing upon hearing a trill and since they typically increase their vigilance, in both this study

and in Weary & Kramer's (1995) playback study, hypotheses #1 (attract), #7 (sentinel) and #2 (manipulate) can be eliminated. Hypotheses #14 and #15 (attract predators or competitors) are also not supported by receivers' behaviour. Neither potential predators nor competitors of predators were observed approaching shortly after the production of a trill.

Burke da Silva (1994) suggested that trilling served predominantly to inform conspecifics about the caller's state (hypothesis #6) because in her study chipmunks called mainly when they disappeared into refuges (especially holes). I tend to reject this hypothesis for trilling in response to an aerial predator for two reasons. First, despite the strong differences in the context in which the calls are naturally given, playbacks of trills produce similar behaviour (alert posture) to playbacks of chucks and chips but typically with less intensity (Weary & Kramer, 1995). It thus does not seem that trills convey particularly useful information about the caller's state to the receiver animals or at least that they do not seem to adopt behaviour that would enhance the caller's or the recipient's fitness. It therefore does not make sense to evolve and use a different call when chucks would have a similar effect. Moreover, since animals often started to chuck just a few seconds after producing a trill, it seems that trills are unlikely to simply serve to inform that the caller has escaped or to indicate its location because similar information could be obtained from the chucks. In addition, although the evidence is limited because of low sample size, the acoustical characteristic of trills produced by the same individual

varied extensively throughout the same trial apparently just as much as individual differences. This is against the prediction that calls of the same individual should be similar in at least some key parameters to allow for individual recognition. Of course chipmunks might be able to perceive more subtle clues that I did not measure.

Since trills are produced by animals directly being pursued by a predator or when the predator appears to be about to pursue them, the two most likely functional explanations of trilling are that calls are either produced to startle the predator (#8) or to inhibit pursuit (#9). The results of this study are in agreement with the predictions of the two hypotheses: 1) trills are produced while the predator has detected the prey and poses a serious threat and while the prey is fleeing or is about to do so, 2) they are produced by individuals of any gender, age and distance to the burrow and 3) the calls should be readily detectable to predators since they cover a wide frequency range (Klump et al., 1986) and should be readily localizable since their spectograms tend to be more vertical than horizontal (Marler, 1955; 1956). The effect of trills on the behaviour of the recipient could not be determined using our experimental set-up because the kestrel was trained to fly in a specific path and was not actually hunting.

Based on a number of lines of evidence, I tend to favor hypothesis #8 (startle). Trills were often produced during a chucking bout immediately following a disturbance. It seems that trilling to advertise that the prey is vigilant to inhibit pursuit (#9) within a chucking bout is a bit unnecessary and redundant since chucking animals are also likely to be vigilant (chucking chipmunks are almost constantly oriented and staring toward the predator). On the other hand, trilling was strongly associated with escape and moving events. These are the cases where to startle the predator (for example, to allow the prey to escape safely or to conceal its a new refuge) would be most useful. Other possible evidence in favor of this hypothesis is obtained from observations concerning the acoustic characteristics of the trill which fits the description of startling calls very well. Such calls are usually single notes or the first few notes of a multiple note call. They are not long lasting, repetitive nor rhythmic vocalizations; otherwise, they would lose their startling effect (Perrins, 1968). The fact that there is so much variation between them even when produced by the same individual is also in favor of a startling function. It prevents habituation by the attacking predator. In addition, trills are produced very unexpectedly which is also typical of startling calls. Tamura & Yong (1993) observed that an aerial predator missed capturing a Malaysian *Callosciurus* squirrel possibly because the latter gave a call consisting of rapid multiple notes just as the predator was swooping down.

Chuck

As seen in this study, chucks are notes, each often comprised of two components that are repeated in prolonged bouts. The first component is of higher frequency and typically has a greater variation in frequency than the second component. It is also acoustically more variable. It does not appear to be a harmonic of the second component, even if one considers the possibility of temporal

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displacement as a result of echoes and effects of attenuation and distortion from other sources. Very clear harmonics of the second been observed at their component have sometimes expected positions along the presence of the new component. The apparently simultaneous production of the two components observed in some cases may suggest some kind of "second voice" phenomenon as observed in some birds. The number of components, their variation in frequency, their extreme and peak frequencies, the time interval between the components and the number of harmonics of component 2 present are extremely variable among individuals but are quite consistent during the chucking period of an individual.

The chuck call of chipmunks has been described, at least briefly, by a number of authors (Seton, 1929; Allen, 1938; Dunford, 1970; Neidhart, 1974 (cited in Elliott, 1978); Elliott, 1978; Burke da Silva et al., 1994). However, until recently, it was not clear whether the chip and chuck calls represented different calls as some thought (Allen, 1938; Neidhart, 1974 as cited by Elliott 1978; Elliott 1978) or were part of a continuum (Damon, 1941; Dunford, 1970; Yahner, 1978). More recently, Burke da Silva et al. (1994) concluded that chip and chuck are distinct calls, based partly on the fact that she found no overlap in frequency in the two calls. The findings of this study shed some light on how this discrepancy could have arisen. The fact that chucks have sometimes only a single component (component 2) and sometimes two components with one similar to the chip call might have confused some authors. Some sonagrams of component 1 resemble sonagrams of the chip calls in Burke Da Silva et al. (1994,

Fig. 1 a and b) and Dunford (1970. Fig. 7 A) but with a lower maximum frequency. In addition, they are quite similar to the sonagrams of the two chips of a chipping bout illustrated by Dunford (1970. Fig. 7 D). The sonagrams of chucking presented by Elliott (1978; Fig. 27) and by Burke da Silva et al. (1994; Fig. 1 c and d) are both similar in structure and within the frequency range of the second component found in this study of chuck. In addition, the sonagrams of one chip of a chipping bout published by Dunford (1970; Fig. 7 E) is similar to some of the sonagrams produced in this study in both structure and in frequency: it has two distinct components and both of them are in similar frequency and duration ranges as our components. In addition, as can be observed in Fig. 7 c of this study, animals sometimes, though rarely, change from a chuck with one component to one with two.

It is surprising that our high frequency component was not observed by Burke da Silva et al. (1994) who recorded from the same chipmunk population a few years earlier. This could be a result of recording differences (e.g., shorter distances in this study) or of differences in stimulus (a living kestrel landing near the animal vs a model swooping overhead). Indeed, differences in stimulus have been shown to influence the acoustical characteristics of calls of one sciurid (Slobodchikoff et al., 1991) as well as various bird species (Klump & Curio, 1983; Ficken, 1990; Evans et al, 1993).

The relationship between chucking and the presence of aerial predators had not been widely recognized before Burke da Silva et al.'s (1994) study. Seton (1929) suggested that chucking was related

to the "erotic impulse". Allen (1938) concluded that chipmunks were not frightened by a hawk circling overhead since they continued chucking for 15 min! Neidhart (1974, as cited by Elliott, 1978) suggested that chucks were produced in response to general disturbances in the habitat. Chucking was first recognized as a response to aerial predators by Elliott (1978) who noted that chucking normally occurred following the flight paths of raptors. Burke da Silva et al. (1994) showed a consistent association between chucking and presence of raptors and other birds. In addition, they experimentally confirmed the association using a model of a hawk as the stimulus. This study confirms that chucking is the only repeated call given in response to an aerial predator. All chipmunks tested chucked at some time during the trial and none chipped except a juvenile that switched from chucking to chipping when an adult appeared and started chipping possibly in response to movements of the observers. In contrast to trills, which are given while escaping a dangerous situation, and to chips, which are produced in the presence of terrestrial predator, chucks are produced in low alarm situations where the predator is perched or has flown away and is typically produced while the caller is stationary.

The use of two distinct repetitive calls is not typical in sciurids. Like eastern chipmunks, chipmunks of the former genus *Eutamias* emit both chucks and chips but no association between call produced and predator type has been detected. Their chucking calls are made of a component bearing some similarity with the component 2 observed in this study in terms of frequency range and presence of

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harmonics but it is longer in duration and given at a higher rate (Brand, 1976). The Columbian ground squirrel is the only other species of terrestrial sciurid reported to use a different repetitive call in response to aerial and terrestrial predators. In the presence of aerial predators, it repeats a hollow chirp slightly higher in frequency than the second component of our chucks (Harris et al., 1983: Lickley, 1984: MacWhirter, 1992). On the other hand, many other ground sciurids produce specific calls which are not repetitive in response to aerial predators. For example, Uinta ground squirrel, Citellus armatus, (Balph & Balph, 1966) and Richardson's ground squirrel (Davis, 1984) emit a chirp-like call (often referred to as a whistle by other authors) while Arctic ground squirrels, Citellus undulatus, (Melchior, 1971) and California ground squirrels (Owings et al., 1977; Owings & Virginia, 1978) give a whistle-like call to aerial predators. The use of different repetitive calls in presence of aerial and terrestrial predator by some sciurids and not by others may reflect differences in function of those calls.

Repetitive calling such as chucking seems to be a very costly activity. Most chipmunks spent considerable time chucking. They usually chucked, sometimes intermittently, for about 15 min and up to more than 30 min. Although it is possible that the chucking bouts in this study were unusually long because the predator remained perched in the vicinity, observations of real natural encounters also suggest that even when an aerial predator has moved on, chipmunks continue to chuck for long periods. Indeed, 5 chipmunks observed in the field reacting to the flight of an aerial predator chucked for more than 7 min (a bit more than 7 min and 15 min 29 s in two cases observed by the present author, 1994; approximately 13 min and 23 observed by A. G. McAdam, personal min in two cases communication, 1994; and about 33 min. students on a field course, 1977). Calling for great lengths of time has also been observed in other sciurid species; for example, hoary marmots call for up to 20 min (Noyes & Holmes, 1979). Columbian ground squirrels for up to 30 min (Lickley, 1984) and one California ground squirrel was observed calling for more than 1 hour (Loughry & McDonough, 1988). Animals therefore often invest heavily in calling; they spend long periods essentially inactive in terms of maintenance activities while possibly attracting other predators and spending energy vocalizing. It is possibly because of the great cost of chucking that chipmunks eventually stop even if the kestrel was still in the vicinity.

As noted by many authors (Allen, 1938; Dunford, 1970; Elliott. 1978; Yahnner, 1978; Burke da Silva et al., 1994) and observed in this study, several chipmunks often chuck at the same time in the same area. A number of authors (e.g. Seton, 1929; Neidhardt, 1974, cited by Elliott 1978; Burke da Silva et al. 1994) have had the impression that chucking was contagious in that animals sometimes engaged in chucking as a response to chucking by other individuals. This was however not confirmed by any study and experimental evidence tends to discredit this suggestion. Indeed, Burke da Silva et al. (1984) observed that only chipmunks exposed to the sight of a flying model ever chucked and chipmunks exposed to playback of chucks never called (Weary & Kramer, 1995). Moreover, the great majority of animals ever heard chucking during this study were visually located by stationary observers because they were typically perched in prominent locations, facing the predator and nearby. The few animals not visually located could easily have been missed because of obstacles in the field of view of the observer or because they were responding to another predator farther away.

Since all animals produced some chucks, no differences in gender, age and distance to burrow in the occurrence of chucking were observed. Burke da Silva et al. (1994) also reported chucking (and chipping) to be performed by adult and juvenile animals of both sexes. On the other hand, they suggested that chucking probability may be related to the distance an animal is from its burrow based on 3 naturally occurring chucking events where 11 callers were on average 10.6 m from their burrow as opposed to 33.3 m for the 3 non-callers. In addition, Burke da Silva (1994) found a highly significant effect of location on probability of chipping in response to a cat where individuals within their area of primary use had a much higher probability of calling. The difference in observations of effects of distance on chuck production between the two studies is possibly due to differences in stimulus strength while the difference in effect of distance between chip and chuck production might possibly be explained by differences in antipredator call functions.

Although all the individuals exposed to the direct attack of the predator chucked and often adopted very similar chucking location and positions, there were often great variations in their calling behaviour. Indeed, latency to start chucking, duration of the chucking

period, percent of this period actually spent chucking and chucking rate typically varied from one individual to another. These variations were usually not or only weakly associated with age, gender and distance to burrow: 1) at intermediate distances from their burrow, females chucked longer than males, 2) distance to burrow had a marginal effect on adult males (animals close to their burrow tended to chuck for a longer period), 3) juvenile males spent significantly less of their chucking period actually chucking than other classes, 4) males chucked at a significantly higher rate than females at the end of the chucking period and 5) juvenile males were closer to the kestrel than juvenile females at the first chucking location. Similarly, there were often great variations among individuals in the various acoustical variables studied (duration of components, their minimum and maximum frequencies, etc.). Gender and distance to burrow were not associated with these variations (age was not tested because of low sample sizes).

Contrary to Burke da Silva et al.'s (1994) impression that chipmunks closer to a terrestrial predator chipped at higher rate, the proximity to the aerial predator did not significantly influence calling rate. In contrast to our findings that rate was not influenced by distance to burrow, Burke da Silva (1994) found that chipmunks within their area of primary use chipped at higher rates. On the other hand, chucking rate differed over the course of the chucking period. The chucking rate at the end of the period was significantly lower than at the beginning or middle. A decrease in rate of calling with

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time was also observed in California ground squirrels (Owings & Virginia, 1978; Loughry & McDonough, 1988).

Functions of chucking

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Similar to trills, a number of hypotheses concerning the function of chucking can apparently be ruled out based on failure of their predictions (see Table 1). On the basis of context of call production, hypotheses #1 (attract), #2 (manipulate), #6 (inform on caller's state), #8 (startle) and #13 (defence) can be rejected. Indeed, from Burke da Silva's (1994) and our observations of natural encounters, chipmunks often continued to call long after the predator had departed the area. They typically called for long periods with no modification of their behaviour while stationary and not about to flee. Moreover, chipmunks never chucked or they stopped calling when the predator posed serious threats (in pursuit or when about to do so) and they often stopped calling when they started performing new activities. It is when predators are threathening that those calls would be most useful. In addition, hypotheses #9 (deter pursuit) and #12 (pursuit invitation) can also be refuted because chucks are often given after the predator has disappeared. In those cases, chipmunks could not possibly know the location of the predator while the predator could locate the caller, making calling very dangerous. Evidence about the caller's identity also leads to the rejection of some hypotheses. Since all individuals called, we can suggest that calling provides a universal selective advantage and exclude kin selected call. Therefore hypotheses #3 (warn), #5 (teach), #7 (sentinel) and #10 (distract) can be eliminated. Characteristics of the chuck call also

suggest rejection of a few hypotheses. Chucking consists of very repetitive vocalizations covering a great frequency range. Hypotheses #3 (warn) and #8 (startle) can therefore be ruled out. First, the structure of chuck notes are not similar to the ones which should be given as warning calls (Marler, 1955; 1956) since the frequency range of these notes is quite audible to avian predators (Klump et al., 1986). More importantly, warning and startling calls consist typically of single notes or the first notes of multi-note calls because repetitive vocalizations reach already alerted individuals (Owings & Virginia, 1978; Greig-Smith, 1980) and are not startling (Perrins, 1968). In addition, we have observed in this study that trills are given in most cases only a few seconds before the first chuck produced by an animal and thus trills are more likely to serve those functions. Moreover, startling calls are produced unexpectedly which is not the case for the rhythmic chucks.

Based on the rationale that chuck production is extremely costly in terms of energy, time and risks of being detected by additional predators, we can also suggest rejection of a number of chuck production hypotheses where effects on the receiver have not been observed. Hypothesis #1 (attract) can be ruled out since it is only in a minority of cases that conspecifics came to the experimental site while a tested animal was chucking. In addition, the possibility that those animals were simply passing by or were already present in the area and thus that they were not directly attracted by a chucking chipmunk cannot be refuted. Moreover, playback of chucks did not attract other chipmunks to the test area (Weary & Kramer,

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1995). Similarly, since conspecifics were never observed fleeing upon hearing chucks and since predators or competitors of the predator were never seen in or coming toward an area where a chipmunk was calling in all of the hours in the field, hypotheses #2 (manipulate) and #14 and #15 (attract predator or competitors) can be discarded. Indeed, it does not make sense that animals would invest as much time and energy as they do if their success is so rarely perceived. Benefits to the caller must be great, otherwise selection would be against such a costly call production. In addition, the fact that predators were never observed pursuing a calling chipmunk contradicts hypothesis #12 (invite pursuit) while it favors hypothesis Since playback of chucks to chipmunks **#9** (deter pursuit). experiments by Weary & Kramer (1995) revealed that the level of vigilance was increased in recipients upon hearing those calls, we can also reject hypothesis #7 (sentinel) which predicts the opposite effects.

The two most likely functional explanations of chucking seem to be hypotheses #4 (maintain vigilance) and #11 (reduce likelihood of later attack). Indeed, repetitive calls such as chucking could serve to maintain a level of vigilance against future attacks as well as to induce the predator to leave the area for another where chances of successful hunting will be greater. The former hypothesis seems less likely than the latter. Indeed, one assumption of this hypothesis is that callers will gain by increasing the vigilance of neighbours so that they rapidly warn the caller if the predator returns but then it does not make much sense for a group of chipmunks to be calling, as is often observed, when a single individual would suffice. Besides, continually repeating a call that is easy to locate when the position of the predator is unknown and when there is only one caller (such as was also observed) seems very risky even when neighbouring animals might be vigilant. On the other hand, chucks were found to increase the level of vigilance in receivers (Weary & Kramer, 1995), and Loughry & Mcdonough (1988) found that vigilance can be maintained over great periods with repetitive calling although long bouts may be proportionally less effective than short ones.

I favor the hypothesis that these vocalizations serve to mob the predators vocally to deter them from hunting in the area. This hypothesis is supported by a number of lines of evidence. The first argument is how conspicuous these individuals tend to be. Indeed, chucking chipmunks typically occupy very obvious positions on perches and are within sight of the predator. They also always remain quite close to the predator while chucking even after a few changes of position, and calling chipmunks orient themselves toward and stare at the predator or where it disappeared as opposed to other directions where conspecifics might be. In addition, chucking bouts sometimes involved several individuals at a time which would not be necessary if chucking served functions other than to mob the predator. A second argument is that animals of all age and gender categories were as likely to call since a call detering the predator to hunt in the area would bring benefits to all. On the other hand, we would have expected that chipmunks farther from their burrow would be less likely to call. Close residents are more likely to face a

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predator returning in the area to hunt and thus have more to gain by chasing it away. This lack of a difference is possibly due to the fact that aerial predator covers a great hunting area very quickly and may leave it and return frequently. An animal living in a burrow 30 or more meters away probably feels as threathened by the return of the predator since this one may travel over its home range. This possibility that the predator's hunting area will overlap with the animal's home range leads to an incentive for calling. A third argument in favor of hypothesis #11 is that chucks are easily detectable (Klump et al., 1986) by the predator because of their wide frequency range. In addition, chucks have sharp onsets and terminations. broad-band and repetitive and are have low frequencies which are features that favor localization (Marler, 1955; 1956). Calls with high detectablility and localizability such as chucks are characteristics of mobbing vocalization (Klump & Shalter, 1984). Although I could not demonstrate from my study that there was a modification of the behaviour of the kestrel when facing chucking chipmunks (since they were tethered), and thus that predators would actually give up the hunt after the prey starts to chuck, there is evidence in the literature that aerial predators do not attempt to attack after a prey has noticed their presence (Morse, 1973; MacDonald & Henderson, 1977; Leger et al., 1980) and many authors (e.g. Rudebeck, 1950, 1951; Kenward, 1978; Barnard, 1979) have argued that they rely on surprise to catch their prey. More importantly, a number of studies have found that predators modify their behaviour when mobbed and have demonstrated that mobbing can in some instances deter predators from hunting (Kruuk, 1964;

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Hoogland & Sherman. 1976; Bildstein. 1982; Buitron. 1983; Pettifor. 1990). For example. European kestrels (*Falco tinnunculus*) mobbed by various species of birds travelled significantly further between hunting locations (perches and windhovering positions) than when undisturbed. In addition. Wilson & Weir (1989) reported that birds of prey such as sparrowhawks repeatedly return to areas where they have been successful in previous hunts. For this reason, it seems very important to reduce the predator's chance of success and to deter it from hunting in the area. Chucking animals, by increasing the vigilance of their conspecifics (Weary & Kramer, 1995), are likely to reduce the hunting success of predators and the likelihood of their return which otherwise could possibly result in the death of the caller.

Conclusions

In summary, we can observe that the general antipredator behaviour of chipmunks in response to avian predator attacks is to trill while running to a closeby refuge and to start chucking for long periods after a very brief hiding period. No major differences among individuals of different ages, genders and distances to burrow were observed. The acoustical characteristics of the trill and both the newly observed and the previously recorded components of the chuck call were described, and no major differences were observed between adults of both genders. It was suggested that the most likely functions of trilling and chucking are respectively to startle the predator and to deter it from hunting in the area since our observations are either in contradiction with the predictions

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associated with the other hypotheses or provide little or no evidence to favor them. On the other hand, many of the predictions concerning the effect of calling animals on the behaviour of the predator could not be accepted or rejected with certainty. Future studies should thus try to shed light on the effects of calling prey on predators.

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Appendix 1

Two natural "attacks" were witnessed from the initial response of a chipmunk to its return to normal behaviour. A summary of these observations is provided in the next few paragraphs as well as a summary of the reaction of the same chip.nunks in response to the kestrel attack to show how similar the behaviour of each animal was during the real and the staged situation. In the first natural situation, an unidentified bird of prey flew toward the chipmunk (an adult male) at an angle of 45° and at a distance of about 20 m and a height of about 15 m. The chipmunk did not move or trill but started chucking almost immediately. It chucked at a rate of 2.1 notes/s for the first 5 minutes after which the rate fell to 2 notes/s. Finally, in the last minute of the chucking bout the rate was 1 note/s. The total chucking duration was a bit more than 7 minutes and in a single bout. The animal was initially on a root (5 cm high) and never moved from it. All 4 paws were touching the ground and it was facing mostly in the direction toward which the bird had disappeared but it moved its head a few times.

The same individual was tested 21 minutes after this real encounter. This time it did trill and run to a refuge where it was almost completely hidden. It moved once to perch itself on the same root as the previous encounter but a bit higher (10 cm above the ground). At the beginning and in the middle of its chucking bout, this animal was chucking at a rate of 2.50 notes/s while at the end of its bout, it was producing 2.20 notes/s. Its head orientation and its paws position was not observed throughout the trial but most of its known orientation was toward the bird and on its four paws. The animal chucked for 167 s.

The other natural event also involved an aduit male. It occurred when another bird flew at a height of about 10 m and a distance of 15 m from an observed chipmunk in a direction parallel to one coming straight toward it. This individual ran about 1.50 m to a hole in a tree but did not trill. At the beginning of the chucking bout, it was chucking at a rate of 2.0 notes/s while in the middle and the end of its bout, it was producing respectively 2.9 notes/s and 2.2 notes/s. It moved only once to perch itself at a height of 38 cm on a fallen branch 2.30 m from its previous position. It spent most of its time with all four paws contacting the substrate and looking either straight toward or 60° to the left of where the predator had disappeared. Again, there was only one chucking bout which lasted 15 minutes and 29 s (929s) and the animal moved away 2 minutes 20 s after it stopped chucking.

This same animal was then tested a bit more than 13 minutes later. This time the animal trilled and ran to the same refuge and after 3 minutes 13 s it moved to the same perch as in the natural situation described above. As in this situation, the individual spent most of its time chucking with all four paws on the substrate and looking either straight toward the bird or 60° on its left. It chucked at a rate of 1.4 notes/s almost throughout the trial and for 144 s and then moved away.

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Table 1. Hypothesized functions of antipredator calls (with the first author to have suggested each function) and predicted patterns of 1) call context, 2) caller characteriatics, 3) call characteristics and 4) effects on receivers

Hypothesized function	Predictions
A) Signal directed to conspecifics	
1) Attract conspecifics to rescue caller or drive predetor away (Hamilton, 1971)	1) given when predator is detected 2) all should call, especially when closer to predator
producer andy (rianinos), 10717	3) cells should be detectable by conspecifics
	4) conspecifics should form groups in response to call
2) Manipulate conspecifics to flee, thereby	1) given by exposed prey before fleeing
distracting predator from caller (Charnov	2) all should call if conspecifics present
& Krebs, 1975)	3) calls should be detectable by conspecifics
	4) conspecifics should take flight in response to call
3) Warn conspecifics of predator (Hamilton, 1964)	1) given when predator is detected
	2) individuals with nearby relatives should call more
	3) calls should be detectable by conspecifics
	4) conspecifics should adopt antipredator behaviour in response to call
4) Maintain (tonic) vigilance to improve detection	1) given when predator is detected and moves away
of returning predator (Schleidt, 1973)	2) all should call
	calls should be repeated and detectable by conspecifics
<i>t</i> :	4) conspecifics should be more vigilant in response to call
5) Teach predator recognition (Curio, 1978)	1) given while young are inexperienced with predators
	2) parents should call more, juveniles less
	3) calls should be detectable by conspecifics
,	4) young should learn to adopt antipredator behaviour

Table 1. Continued.

Hypothesized function Predictions A) Signal directed to conspecifics (continued) 6) Inform on caller's state (e.g. hiding but safe) 1) given when state of caller will become ambiguous (Burke da Silva, 1994) 2) all should call 3) calls should allow for individual recognition 4) conspecifics should modify their behaviour 7) Inform that caller is vigilant (sentinel) so that 1) given when predator is likely to be in the area others can perform normal activity (Morton 2) individuals with nearby relatives should call more & Shalter, 1977) 3) calls should be repeated and detectable by conspecifics 4) conspecifics should be less vigilant in response to call B) Signal directed to predator 1) given unexpectedly while under serious threat 8) Startle the predator (Perrins, 1968) 2) all should call 3) calls should be detectable by predator and not repetitive 4) predator should be more likely to miss an attack in response to call 9) Deter pursuit by predator (Zahavi, 1977) 1) given by exposed prey about to flee 2) all should call, especially when closer to predator 3) calls should be localizable by predator 4) predator should be more likely to give up the attack 10) Distract from vulnerable individuals (Klump 1) given when vulnerable individuals are exposed & Shalter, 1984) 2) relatives should call more 3) calls should be detectable by predator 4) predator should be diverted to the caller

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Table 1. Continued.

Hypothesized function Predictions B) Signal directed to predator (continued) 11) Reduce likelihood of later attacks by inducing 1) given when predator is nearby but not attacking predator to hunt elswhere (Trivers, 1971) 2) residents should call more 3) calls should be detectable by predator 4) predator should leave the area in response to call 12) Invite pursuit of the caller (Smythe, 1977) 1) given when predator is nearby but not attacking 2) caller should be in a position to escape 3) calls should be localizable by predator 4) predator should attack more readily in response to call 13) Scare the predator (Klump & Shalter, 1984) 1) given by a caller defending itself from a predator about to attack 2) stronger, healthier individuals should call more 3) calls should be localizable by predator 4) predator should attack less readily in response to call

C) Signal directed to other individuals

- 14) Altract predators of the predator possibly resulting in prey escape from flight of its predator (Nicolai, 1973 as cited by Curio, 1978)
- 15) Attract competitors of the predator possibly resulting in prey escape during attempted kleptoparasitism (present study)

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- 1) given more for predators with more predators
- 2) all should call
- 3) calls should be detectable by different predators
- 4) other predators should be attracted in response to call
- 1) given more for predators at risk of kleptoparasitism
- 2) all should call
- 3) calls should be detectable by kleptoparasites
- 4) competitors should be attracted in response to call

Table 2. Data recorded during and after trials.

Observations made in the field during a trial:

- 1. Date of the trial
- 2. Time at start of trial
- Site: study area divided into 7 sub-areas in turn divided into regions
- Habitat characteristics: distance to public path, tilt of the area, vegetation level (each aspect was given one of three order of magnitude; low, middle and high level)
- 5. Weather: general description of the weather during the experiment (sunny, cloudy, windy, warm, cold)
- 6. Light level: heavily shaded, moderately shaded, lightly or unshaded
- 7. Trill: presence or absence
- 8. Trill timing: did the chipmunk trill early (before or while starting its flight) or late (after it had clearly started to run)?
- Refuge type: any type of structure attained by the chipmunk at end of its first flight. It could provide complete or only partial protection.
- 10. Emergence time: time at which the chipmunk emerged from its refuge. When an animal hid in refuges that made it visible at all time, emergence time was considered the moment the animal moved thus becoming more visible.
- 11. Chucking: presence or absence
- 12. Time of the first chuck

Table 2. Continued.

Observations made in the field during a trial: (continued)

- 13. Start of first chucking bout: defined as chucking for more than 3 chucks given at regular intervals
- 14. End of first chucking bout: no chucking for at least 5 seconds
- 15. Subsequent chucking bouts: the time at which any subsequent chucking bouts started and stopped was determined using the same criteria as for the first bout
- 16. Chucking rate (notes/s): rate of chucking during chucking bout taken about every 30 s for an average duration of 15 s
- 17. Time of the start and end of a new activity: time at which the chipmunk changed its activity. Activities included a) grooming,b) moving, c) foraging, d) producing a new call and e) eating
- 18. Time of changes in head orientation: time at which the chipmunk changed its head orientation to a new direction relative to the bird's position. Head orientations included a) within 30° on either side of an imaginary line straight to the predator (facing the predator), b) in the next 30° to 90° on either side (facing sideways) and c) more than 90° (facing away).
- 19. Time of changes in the numbers of feet contacting substrate for stationary animals
- 20. Time of disturbance: disturbances included a) wing flapping, b) other movement by the kestrel, c) gusts of wind and d) people approaching

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. . . Table 2. Continued.

Observations made in the field during a trial: (continued)

- 21. Disturbance effects: apparent effect(s) of the disturbance on the chipmunk's behaviour. Effects included a) no reaction, b) decrease in chucking rate, c) stopping to chuck, d) trilling, e) moving, and f) increasing chucking rate
- 22. Final activity: forage, leave the area or stay immobile for more than 5 minutes
- 23. Time of trial end: time at which the animal started foraging, left the area or spent 5 minutes with no calls or movements.
- 24. Presence of non-focal chipmunk: was there any non-focal chipmunk visible or calling during the trial?
- 25. Chucking by non-focal chipmunk: presence or absence
- 26. Time of the first chuck produced by non-focal chipmunk
- 27. Chucking rate of non-focal chipmunk (notes/s): rate of chucking taken whenever possible for an average duration of 15 s

Measurements made directly in the field:

- Distance from box to perch (m): distance travelled by the kestrel during the flight from the starting box to the perch on which it rested
- 2. Distance to burrow (m): distance from the position of the chipmunk at the start of the trial (initial position) to its burrow
- 3. Distance run (m): distance from the initial position of the chipmunk to the refuge at which it first stopped running

Table 2. Continued.

Measurements made directly in the field: (continued)

- 4. Distance to bird when chucking (m): distance between the chucking chipmunk and the bird
- 5. Perch height (cm): height above ground of each perch from which the animal chucked
- 6. Distance to bird of non-focal chipmunk when chucking (m): distance between the non-focal chucking chipmunk and the bird
- 7. Perch height of non-focal individuals (cm): height above ground of the perch of non-focal chipmunks from which the animal chucked

Table 3. Behavioural variables calculated from field observations and recordings.

- Hiding time (s): difference between initial reaction and emergence Post-hiding silent interval (s): difference between emergence time and start of first chucking bout
- 2. Chucking Latency (s): difference between initial response and start of first chucking bout
- 3. Chucking rate at the beginning of chucking period (notes/s): average chucking rate within the first minute of the first bout
- 4. Chucking rate in the middle of chucking period (notes/s): average chucking rate at or closest to the middle point of the total chucking period
- 5. Chucking rate at the end of chucking period (notes/s): average chucking rate within the last minute of the last bout
- 6. Duration of each chucking bouts (s)
- 7. Pause durations (s): difference between end of one bout and start of the next
- 8. Total chucking duration excluding pauses (s): sum of duration of each bout
- 9. Chucking period (s): difference between first bout starting time and last bout ending time
- 10. Percent chucking time (s): ratio of total chucking duration excluding pauses over chucking period, multiplied by 100
- 11. Time spent in each category of head orientation (s): sum of all the time intervals with head orientation in each category

Table 3. Continued.

- 12. Percent time spent in each category of head orientation (s): ratio of time spent in each category of head orientation and duration of first chucking bout, multiplied by 100
- 13. Delay to final activity (s): difference between last bout ending time and time of trial end
- 14. Duration of total response (s): difference between time of the trial start time (time = 0 s) and time of trial end
- 15. Latency to chuck by non-focal chipmunk (s): difference between the trial start time

Table 4. Acoustical variables derived from sonagrams and waveforms.

A. Trills:

- Duration (ms): the difference between the beginning time and the end time of the selected portion of the call (entire call or individual note)
- 2. Minimum frequency (kHz): the lowest frequency of the selected portion of the call
- 3. Maximum frequency (kHz): the highest frequency of the selected portion of the call
- 4. Frequency range (kHz): the difference between the highest and lowest frequency of the selected portion of the call
- 5. Frequency of peak amplitude (kHz): the frequency at which the highest amplitude of the selected portion of the call occurs
- 6. Presence of harmonics: presence of multiples of the frequency at peak amplitude
- 7. Interval between notes (ms): the difference between the end time of a note and the beginning time of the next one
- 8. Time of peak amplitude (ms): the time from the beginning of the call at which the highest amplitude occurs

B. Chucks:

- 1. Presence of component 1: presence of a component-which had frequencies ranging between 2.5 and 10 kHz
- 2. Presence of component 2: presence of a component which had frequencies ranging between 0.5 and 3 kHz

Table 4. Continued.

B. Chucks: (continued)

- 3. Duration (ms): the difference between the beginning time and the end time of the selected component of the note
- 4. Minimum frequency (kHz): the lowest frequency of the selected component of the note
- 5. Maximum frequency (kHz): the highest frequency of the selected component of the note
- 6. Frequency range (kHz): the difference between the highest and lowest frequency of the selected component of the note
- 7. Frequency of peak amplitude (kHz): the frequency at which the highest amplitude of the selected component of the note occurs
- 8. Presence of harmonics: presence of multiples of the frequency at peak amplitude of the component
- 9. Interval between components (ms): the difference between the end time of the first component) and the beginning time of the second

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Table 5. Antipredator responses of chipmunks in relation to age and gender. The table shows either the proportion of animals performing a particular response or the median level and range of response, with sample size in parentheses, for adult and juvenile, female and male chipmunks.

Age and gender categories

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Parameter	Adult females	Adult males	Juvenile females	Juvenile mates	All Individuals
Distance run (m)	2.7 (21)	2.5 (22)	2.8 (6)	2.4 (4)	2.7 (53)
	0.8-5.6	0.7-10.8	0.1-4.3	0.7-4.2	0.1-10.8
Refuge types (%)		-			
1) Burrows	4.8	0	0	25.0	3.8
2) Other holes	9.5	4.6	16.7	25,0	9.4
3) Overhead protection	38.1	31.8	66.7	50,0	39.6
4) Side protection	47.6	54.5	0	0	41.5
5) Leaf litter	0	9.1	0	0	5.7
6) Climb up	0	0	0	0	0
(n)	(21)	(22)	(6)	(4)	(53)
Probability of trilling (%)	90.5 (21)	95.5 (22)	83.3 (6)	75.0 (4)	90.6 (53)
Probability of early trill (%)	89.5 (19)	90.5 (21)	100.0 (5)	100.0 (3)	91.7 (48)
Hiding time (s)	6 (21)	5 (21)	7 (6)	94.5 (4)	6 (52)
	2-1164	2-220	4 -31	4-366	2-1164
Slience interval after hiding (s)	1 (21)	0 (21)	0 (6)	6 (4)	0 (52)
energy and the second sec	-97-5	-106-418	-26-537	-362-13	-362-537
Chucking latency (s)	13 (21)	12 (21)	7 (6)	12 (4)	10 (52)
	2-1164	3-420	4-542	4-194	2-1164

Table 5. Continued.

Age and gender categories

Parameter	Adult females	Adult males	Juvenile females	Juvenile mates	All Individuals
Chucking period (s)	827 (21)	774 (21)	517 (5)	857 (4)	784 (52)
	111-1898	144-1015	7-1027	522-884	7-1898
Percent chucking time (%)	97.8 (21)	96.2 (21)	99.2 (6)	59.0 (4)	96.3 (52)
	45.7-100.0	27.9-100.0	90.3-100.0	42.8.71.6	27.9-100.0
Chucking rate (note/s)					
1) at the beginning	1.3 (21)	2.0 (21)	1.3 (6)	1.0 (4)	1.4 (52)
	0.4-2.4	0.3-2.8	0.5-2.1	0.7-1.8	0.3-2.8
2) at mid-point	1.3 (21)	1.8 (21)	1.3 (6)	1.3 (4)	1.5 (52)
	0.5-2.5	0.7-2.8	0.7.2.7	1 1 1.7	0.5-2.8
3) at the end	0.9 (21)	1.4 (21)	U.9 (6)	1.5 (4)	1.1 (52)
•	0.3-2.3	0.5-2.8	0.6-1.8	1.0-2.0	0.3-2.8
Duration of total response (s)	1035 (21)	880 (20)	905 (6)	1192 (4)	930 (51)
1)	190-1901	229-1470	90-1500	861-1410	90-1901
1) Latency to forage	912 (4)	442 (6)		962 (2)	805 (12)
	758-1199	229-1267		861-1063	229-1267
2) Latency to leave	930 (15)	880 (10)	668 (5)	1321 (1)	887 (31)
	190-1901	434-1062	90-1164	1321-1321	90-1901
3) No new activity	1223 (2)	1195 (4)	1500 (1)	1410 (1)	1223 (8)
•	1200-1245	1020-1470	1500-1500	1410-1410	1020-1500

Table 6. Antipredator responses of chipmunks in relation to distance to burrow. The table shows either the proportion of animals performing a particular response or the median level with sample size in parentheses and range of response for three distance to burrow categories.

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Distance to burrow categories

Parameter	<15.0 m	15.0-29.9 m	>29.9 m	All distances
Distance run (m)	2.7 (31)	2.2 (15)	2.9 (7)	2.7 (53)
	0.7-5.6	0.1-5.3	1.0-10.8	0.1-10.8
Refuge types (%)				
1) Burrows	6.5	0	0	3.8
2) Other holes	12.9	6.7	0	9.4
3) Overhead protection	38.7	53.3	14.3	39.6
4) Side protection	35.5	33.3	85.7	41.5
5) Leaf litter	6.5	6.7	0	5.7
6) Climb up	·/ 0	0	0	0
(n)	(31)	(15)	(7)	(53)
Probability of trilling (%)	87.1 (31)	93.3 (15)	100.0 (7)	90.6 (53)
Probability of early trill (%)	92.6 (27)	85.7 (14)	100.0 (7)	91.7 (48)
Hiding time (s)	6 (30)	6 (15)	5 (7)	6 (52)
	3-1164	2.105	2.8	2-1164
Silence interval after hidind (s)	0 (30)	0 (15)	0 (7)	0 (52)
	-362-537	-97-418	0-44	·362· 537
Chucking latency (s)	12 (30)	11 (15)	6 (7)	10 (52)
	3-1164	3-420	2 - 49	2-1164

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Table 6. Continued.

Distance to burrow categories

Parameter ¹³	<15.0 m	15.0-29.9 m	>29.9 m	All distances
Chucking period (s)	784 (30)	827 (15)	515 (7)	784 (52)
	7-1057	167-1898	111-1297	7-1898
Percent chucking time (%)	96.3 (30)	97.5 (15)	96.5 (7)	96-3 (52)
	27.9-100.0	45.6-100.0	66.7.100.0	27 9-100.0
Chucking rate (note/s)		•		
1) at the beginning	1.3 (30)	1.0 (15)	1.5 (7)	1.4 (52)
	0.3-2.8	0.4-2.5	0.9-2.3	0.3-2.8
2) at mid-point	1.4 (30)	1.9 (15)	1.8 (7)	1.5 (52)
	0.5-2.8	0.9-2.5	0.8-2.5	0 5-2 8
3) at the end	0.9 (30)	1.0 (15)	1.4 (7)	1.1 (52)
() ()	0.5-2.8	0.3-2.3	0.8-2.6	0.3-2.8
Duration of total response (s)	1060 (29)	904 (15)	857 (7)	930 (51)
	90-1490	229-1901	190-1382	90-1901
1) Latency to forage	948 (6)	614 (6)		805 (12)
	414-1199	229-1267		229-1267
2) Latency to leave	963 (16)	956 (8)	857 (7)	887 (31)
• • • • •	90-1490	668-1901	190-1382	90-1901
3) No new activity	1200 (7)	1500 (1)		1223 (8)
_,	1020-1470	1500-1500		1020-1500

Table 7. Acoustical parameters of the trill calls by mate and female chipmunks

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	Females								Males					
Parameter	N	Mean	t	SE	(Min.	•	Max.)	N	Mean	Ł	Æ	(Min.	•	Max.)
Duration (ms)	7	520.08	1	92.64	(97.15	••••	846.09)	7	570.66	Ł	84.58	(295-79		1027-32
Number of notes per call	7	8.43	t	1.57	(3.00	-	13.00)	7	7 57	t	1.25	(3 00	•	13 00)
Interval between notes (ms)	52	54.01	t	8.19	(0.00	•	500.00)	46	65.08	ł	11.81	(0 00		519-00)
Range of Frequencies (kHz)	7	6.25	£	0.71	(2.55	•	8.68)	7	4.70	t	0.29	(3-60	•	5 89)
Minimum Frequency (kHz)	7	2.54	ŧ	0.35	(1.27	•	3.56)	7	3 35	ł	0 44	(1.09		4 45)
Maximum Frequency (kHz)	7	8.78	t	0.53	(6.12	•	10.44)	7	8.05	£	0-38	(6-81		9 25)
Frequency at peak amplitude (kHz)	7	5.72	ŧ	0.32	(5.06	•	7.43)	7	5.90	1	0 47	(5-06		8 52)
Position of note of peak amplitude	7	3.71	£	0.92	(1.00	-	8.00)	7	2.00	t	0.53	(1.00		4-00)
Time of peak amplitude (ms)	7	206.24	t	59.04	(22.81	•	447.56)	7	309-21	ŧ	44-70	(6-94		316-15)
Duration of notes (ms)	59	25.50	1	1.40	(2.00		55.55)	53	19-41	1	087	(6 92		95-89)
Range of Frequencies of notes (kHz)	59	2.77	t	0.23	(0.46	•	6.33)	53	2 64	1	0 16	10-35		4-76)
Minimum Frequency of notes (kHz)	59	4.08	t	0.15	(1.13		7.74)	53	4 42	1	0-16	(1-09		6 85)
Maximum Frequency of notes (kHz)	59	6.84	t	0.19	(1.82		10 21)	53	7 06	ł	0-19	(2-18		9.25)
Frequency at peak amp. of notes (kHz)	59	5.71	t	0.13	(1.50	•	8.02)	53	5 77	:	0 17	(1 50		8521
Number of special notes	5	2.00	t	0.69	(0.00	•	5.00)	2	0 57	:	0-43	(6,65		3
Position of first special note	5	2.80	t	1.35	{1.00	•	8.00)	2	5 00	:	1.00	(4.95	·	•, '

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Table 8. Comparative acoustical characteristics of selected notes of trill calls of chipmunks

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A. Position of the note

	First Note								Last Note						
Parameter	 N	Mean	t	SE	(Min.	•	Max.)	N	Mean	<u>t</u>	SE	(Min.		Max.)	
Position of the note	14	1.00	t	0.00	(1.00	• •	1.00)	14	8.00	<u>t</u>	0 97	(3 00		13 00)	
Duration (ms)	14	26.48	t	3.15	(12.34	-	55.55)	14	16.68	Ł	1.93	(2 00		29-91)	
Range of Frequencies (kHz)	14	3.70	t	0.41	(1.28	•	6.33)	14	t.43	ł	0.23	(0.48		3 58)	
Minimum Frequency (kHz)	14	3.89	Ł	0.19	(2.66	-	5.19)	14	4.67	ł	0.25	(3-10		6 63)	
Maximum Frequency (kHz)	14	7.60	£	0.36	(4.96	-	9.51)	14	6.11	t	0 29	(4-73	•	8 86)	
Frequency of peak amplilude (kHz)	14	5.42	ŧ	0.18	(4.46	-	7.17)	14	5.45	t	0 22	(4 00		7 17)	
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Table 8. Continued.

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B. Duration of the note

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,		Shortest Note								Longest Note					
Parameter	N	Mean	t	SE	(Min.	•	 Max.)	N	Mean	±	Æ	(Min.	•	Max.)	
Position of the note	14	5.61	t	0.82	(1.00	 •	13.00)	14	3.21	Ł	ი.56	(1.00	•	8.00)	
Duration (ms)	14	12.25	t	1.45	(2.00	•	21.37)	14	33.15	t	2.57	(20.76	-	55.55)	
Range of Frequencies (kHz)	14	1.60	±	0.31	(0.48	•	4.76)	14	3.55	£	0.42	(1.31	-	6.33}	
Minimum Frequency (kHz)	14	5.05	t	0.33	(3.14	•	7.74)	14	3.76	£	0.25	(2.57		5.85)	
Maximum Frequency (kHz)	14	6.65	t	0.33	(4.19	-	8.67)	14	7.31	t	0.38	(5.41		9.51)	
Frequency of peak amplitude (kHz)	14	5.76	t	0.30	(3.51	-	8.02)	14	5.93	t	0.30	(5.06		8 52)	
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Table 8. Continued.

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C. Frequency of the note

		Lowest Frequency Note								Higest frequency Note					
Parameter	N	Mean	±	SE	(Min.	•	Max.)	N	Mean	· . 1	Œ	(Min.		Max.)	
Position of the note	14	4.07	t	0.89	(1.00	 -	12.00)	14	3.57	t	0 73	(1.00	·	10-00)	
Duration (ms)	14	24.45	ŧ	2.87	(12.34	•	41.91)	14	26.66	t	3.50	(9.65		55 55)	
Range of Frequencies (kHz)	14	3.44	t	0:46	(1.09	•	5.80)	14	4.10	t	0.48	(0.58		6.33)	
Minimum Frequency (kHz)	14	3.14	Ŧ	0.28	(1.09	-	4.45)	14	4.31	t	0.35	(2.66		7-74)	
Maximum Frequency (kHz)	14	6.58	t	0.48	(2.18	•	9.51)	14	8.41	t	0.32	(6.12	-	10.21)	
Frequency of peak amplitude (kHz)	14	5.19	t	0.35	(1.50	-	7.43)	14	6.27	t	0.29	(5 06		8.52)	
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Table 9. Acoustical parameters of chuck calls by male and female chipmunks

Females Males - ----Parameter N Mean ± SE (Min. - Max.) SE (Min. - Max.) N Mean t Percentage of notes with Component 1 10 88.67 ± 9.90 (0.00 - 100.00)10 84 67 € 8 15 (20.00 100.00) Interval between the Components (ms) 9 0.05 ± 0.03 (0.01 - 0.27)9 0 10 ł 0.09 (0.01 0.79) Duration (ms) Comp. 1 9 16.30 ± 1.39 (8.30 · 21.80) 9 18 26 ± 161 (9.23) 25.80) Comp. 2 10 21.65 ± 2.17 (6.70 · 31.80) 10 21 30 ± 2 20 (12.89 36.50) Range of Frequencies (kHz) Comp. 1 9 2.20 1 0.24 (1.24 - 3.32) 9 186 ± 030 (0.80 3 36) Comp. 2 10 1.13 ± 0.13 (0.36 - 1.70) 10 113 ± 0.09 (0.76 1.68) Minimum Frequency (kHz) Comp. 1 9 4.02 ± 0.18 (2 99 - 4 84) <u>9 4 11 ± 0 11</u> (3.52 4 54) Comp. 2 $10 1.00 \pm 0.09$ (0.77 - 1.78) 10 0.92 ± 0.05 10.67 1.12) Maximum Frequency (kHz) Comp. 1 9 6.23 ± 0.27 (4.69 - 7.37) 9 5 97 ± 0 28 (4 86 7.521 Comp. 2 10 2.13 ± 0.09 (1.65 - 2.59) 10 204 ± 0.09 (1.70 269 Frequency at Peak Amplitude (kHz) Comp. 1 (4 10 - 6 14) 9 5.33 ± 0.19 9 507 ± 019 (4.12) 6.11) Comp. 2 10 1.48 ± 0.07 (1.23 - 1.98) 10 141 + 5.04 11 22 1 . 1 Number of Harmonics in Component 2 (0.00 - 5.00)10 240 1 064 10.55 5 GU 10 2.30 ± 0.58

Figure 1. Equipment set up for kestrel. A) Method of restraining kestrel using bracelets (small rings of leather held by eyelet-holes), jesses (small leather straps knotted at one end and with a hole at the other) and leashes (small thread tied to a snap-hook). B) Set up of the major equipment in the field. At the beginning of a trial, the door of the box on the step-ladder was opened by releasing the fishing line. The kestrel would then fly over a patch of seeds (dots) toward its ground perch and its lure. The flight was guided by another fishing line along which a small ring tied to the jesses of the bird could move freely.



Figure 2. Time spent hiding by adult (a) and juvenile (j) chipmunks choosing different refuge types. Abbreviations for refuge types: B =burrows, H = holes, L = leaves. O = overhead cover and S = side protection. The median is represented by the center line and the edges of the box plot represents the lower and upper quartiles. The vertical lines extend from the upper and lower quartiles to 1.5 interquartile ranges (the absolute value of the difference between the values of the two quartiles) or up to the most extreme value within this range. Asterisks indicate values that lie between 1.5 and 3 interquartile ranges from the box. Sample sizes (number of individuals) are shown for each category.



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Figure 3. Chucking period for female (F) and male (M) chipmunks in relation to distance to burrow. Distance to burrow was divided into 3 categories: Near = 0 - 14.9 m, Middle = 15.0 - 29.9 m, and Far > 29.9 m. Box plots as in Fig. 2.

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Figure 4. Percent of time from the beginning of the first chuck of the first chucking bout to the last chuck of the last chucking bout spent chucking by adult and juvenile, female (F) and male (M) chipmunks. Box plots as in Fig. 2.

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Figure 5. Orientation of chipmunks during their first chucking bout in relation to location of the kestrel. The figure shows mean percent time that 42 adult and 10 juvenile chipmunks of both genders spent oriented within 30° on either side of an imaginary line straight to the predator (facing the predator). or in the next 30° to 90° on either side (facing sideways) and more than 90° (facing away)). NV shows the percent time not visible to the observer.



Orientation relative to predator

Figure 6. Sonagrams of trills of two individual chipmunks illustrating variation in note form and interval. Sonagram A is from male #22, recorded 20 September 1994, with the last three notes characterized by an increasing frequency before the decrease. Sonagram B produced by female #27 on 20 September 1994 illustrates a very different call even though the number of notes is the same. Great differences in interval length between notes can be observed and notes cover a low frequency range.



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Figure 7. Sonagrams of two chuck calls from different parts of a chucking sequence by three different male chipmunks. (A) Chipmunk #53 (recorded 1 October 1994) is an example of an animal with only the second component of the chuck. The examples were produced at the beginning and end of a chucking bout lasting 769 s. (B) Chipmunk #93 (recorded 21 September 1994) illustrates a chipmunk with both first (C1) and second (C2) components in its chuck. The examples were produced 637 s apart during different bouts separated by two changes of location. (C) Chipmunk #73 (recorded 23 September 1994) illustrates an animal that switched from a chuck with the second component only (C2) to one in which the first component (C1) was also present during the course of a chucking bout. It also provides a good example of harmonics (H1 and H2) of the second component. Note that the first harmonic of the second component partially overlaps the first component. The chucks illustrated were separated by 62 s and produced during the same bout.

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