

eScholarship

International Journal of Comparative Psychology

Title

Individual Modulation of Anti-predator Responses in Common Marmosets

Permalink

<https://escholarship.org/uc/item/9wp5d6tz>

Journal

International Journal of Comparative Psychology, 24(1)

ISSN

0889-3675

Authors

Kemp, Caralyn

Kaplan, Gisela

Publication Date

2011

DOI

10.46867/ijcp.2011.24.01.02

Copyright Information

Copyright 2011 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

Individual Modulation of Anti-predator Responses in Common Marmosets

Caralyn Kemp and Gisela Kaplan
University of New England, Australia

Group living may confer an advantage on prey animals if individuals help maximise protection from predation. Some evidence suggests that age and sex differences may signify role divisions in fight/flight responses. We examined whether captive common marmosets (*Callithrix jacchus*), a group-living primate species, might also show sex and age differences in response to predators and presented predator-based visual and auditory stimuli, individually and simultaneously. No significant sex or age differences emerged in any of the behaviour recorded. However, we found strong evidence that there were individual differences in flight/fight responses depending on the stimulus presented. In presenting a taxidermic model of a carnivore visually, five (of the 12) marmosets showed behaviour suggesting cautiousness, whereas five other marmosets displayed risk-taking behaviour (scored as close proximity to stimulus, mobbing vocalisations and short latency to approach and vocalise). Importantly, cautious and risk-taking individuals did not behave consistently in these roles but changed when presented with the auditory stimulus or the visual and auditory stimuli combined. These results suggest that there may be individual differences in assessing sensory cues and levels of fearfulness and risk-taking may vary accordingly. Whether or not such differences confer an advantage on group living species, it is an entirely new finding that the type of sensory stimulation affects and alters behaviour to a significant extent within an individual and within the same group of primates.

This paper reports responses by common marmosets (*Callithrix jacchus*) to visual and auditory stimuli signalling predators. We were interested to see how individual members of this group-living species would respond when auditory and visual stimuli were presented separately or simultaneously. We also presented conflicting visual stimuli (a favourite food item placed near a predatory model) to assess the strength of responses to risk, similar to the classical study by Skals, Anderson, Kannevorff, Löfstedt, & Surlykke (2005) on the strength of conflicting stimuli presented to male moths (pheromones of a female moth versus artificial bat vocalisations). Predation has long been regarded as a major force in shaping the behaviour of animals (Isbell, 1994; Lima & Dill, 1990), including social structure, group composition, vigilance, vocal behaviour, and ecological niche (Cheney & Wrangham, 1987; Isbell, 2006; Stanford, 1998; Uster & Zuberbühler, 2001; van Schaik, 1983). Yet there is also evidence that predation pressure is not equal for all individuals within a group (for example, juveniles are more susceptible than adults, surplus males may be pushed to the perimeter of a group where the risk of predation is greater; Caro, 2005). It is therefore of some importance to ask whether and to what extent, if any, sex, age and individual differences influence anti-predator behaviour.

Animals obtain information about predators using sensory processing in different modalities. At present, we know relatively little as to whether a single modality may provide the important trigger to respond (primates are considered to be visually orientated; Laska, Seibt, & Weber, 2000), or whether the perceived

information in a particular sensory cue interacts in a specific way with another cue to elicit a response (Martin, 1990). In addition, a single sensory stimulus may contain multiple cues. For example, predator vocalisations, between species and within, may differ in pitch, amplitude and frequency. These cues may provide the prey animal with specific information about the size, state and hunting readiness of a predator. Different information may also be perceived between sensory stimuli of different modalities. Visual, auditory and possibly olfactory cues of a predator may provide sensory-specific information about relative proximity (auditory), type (visual or auditory) or distance in time (olfactory) of a predator, or contain other differences in qualitative information, even when originating from the same source (Møller & Pomiankowski, 1993).

Predictions of possible responses to different sensory cues from the same stimulus have led to a variety of theoretical positions, which have remained largely untested (Meredith & Stein, 1983; Partan & Marler, 1999; Stein, Huneycutt, & Meredith, 1988). For instance, the threat-sensitivity predator avoidance hypothesis (Helfman, 1989) suggests that a combination of related sensory cues may have an additive effect, whereas other theories suggest that, when the different cues provide different information, despite originating from the same source, the behavioural response will be modified (Partan & Marler, 1999, 2005; Stein & Meredith, 1993). For their survival, animals need to use and respond to the information provided in a sensory cue and assess their risk of predation accurately (Lima & Dill, 1990). Clearly, multiple cues ought to provide an animal with a greater ability to recognise the predator, to assess the predation risk accurately and to respond perhaps more quickly and effectively than they otherwise would have been able to do (Amo, Lopez, & Martin, 2004, 2006; Hartman & Abrahams, 2000). However, the question remains which type or modality of signal, or cue within a signal, elicits a specific response, whether, when presented separately each leads to an entirely different response patterns or, in combination, results in faster or even slower, hence contradictory, behaviour (modifying freeze/flee responses).

The research history on responses to predators has been characterised by a single sensory approach (Partan & Marler, 1999). Yet Darwin (1872) suggested that multiple, concurrent stimuli should be important in the perceptual and communication systems of animals, a theory which Tinbergen (1959) reiterated. It has been widely acknowledged that many signals in nature are multimodal and are conveyed via multiple sensory channels (Guilford & Dawkins, 1991; Rowe & Guilford, 1999). In recent years, it has been argued more strongly that sensory modalities may not always work independently of each other (Hebets & Papaj, 2005; Partan & Marler, 1999; Rowe & Guilford, 1999; Smith, 1994). Therefore, it was important to our study that multiple sensory cues were used when testing the response of individual marmosets to predatory stimuli.

The common marmoset is an ideal species for exploring multimodal processing of aversive/predatory cues for a number of reasons. Marmosets have excellent vision (Troilo, Howland, & Judge, 1993) and a wide hearing range (Seiden, 1957). They live in small to large family groups and may need to defend themselves against conspecifics, other animals or predatory threats. As is well documented, Callitrichids, to which *C. jacchus* belong, are a group of New World

primates at risk from a diverse range of potential predators, such as raptors and other birds, snakes, felids, and tayras due, largely, to their small body size (Bezerra, Barnett, Souto, & Jones, 2009; Heymann, 1990; Rylands, 1981).

We already know that this group living prey species has developed a wide array of behavioural adaptations for maximising predator detection (Caine, 1993) and minimising predation risk (Ferrari & Lopes Ferrari, 1990; Heymann, 1990). One such behaviour is vigilance, which has been observed in common marmosets in the wild (Rylands & de Faria, 1993), and other Callitrichids (Hardie & Buchanan-Smith, 1997). Vigilance, which includes the visual scanning of the environment for potential threats (Bednekoff & Lima, 1998), is a step in a chain of anti-predator strategies that marmosets may utilise to avoid predation. A second step may be warning others or deterring the predator by means of specific vocalisation; marmosets often use mobbing vocalisations, in particular the 'tsik' call (Clara, Tommasi, & Rogers, 2008; Epple, 1968). In the case of aerial predators that cannot be mobbed marmosets tend to freeze or flee upon hearing a raptor vocalisation to avoid detection, monitoring the bird if it can be seen (Searcy & Caine, 2003; Ferrari & Lopes Ferrari, 1990). Some instances of predator avoidance have been reported for potential terrestrial predators of marmosets in the wild (Ferrari & Lopes Ferrari, 1990) and predator avoidance has been described as a common response of captive marmoset populations that have little or no exposure to predators (Barrose, Boere, Mello, & Tomaz, 2002). Thus even in captive contexts, there are a range of measurable behavioural responses (such as vocalisations, latency to approach, fight/flee responses and distance to predatory cues) that can be scored when marmosets are faced with a visual predator cue.

The controversial aspect of testing marmosets in captivity on predator recognition has always been the question as to how meaningful such testing might be if these captive marmosets, especially those that are held in indoor facilities without exposure to any potential predators, were entirely predator naïve prior to testing. The marmosets in this study had been captively reared for many generations and while our testing group had access to outdoor cages, the opaque roof and the limited views of the outside world afforded little opportunity to see or hear any species which might pose a risk to marmosets, let alone gather any experience with such predators. Previous studies that tested the ability of Callitrichids to visually recognise predators, using either live or sculpted/taxidermic models (e.g., Barros, Boere, Huston, & Tomaz, 2000; Barros et al., 2002; Caine, 1998; Clara et al., 2008; Dacier, Maia, Agostinho, & Barros, 2006; Hayes & Snowdon, 1990) had conflicting results concerning the level of experience necessary for such recognition. In some cases (e.g., Campbell & Snowdon, 2009), the predator-naïve primates showed no difference in their behaviour to any of the stimuli presented, regardless of whether or not it was actually a) a predator, or b) a predator of the prey species being tested. For instance, marmosets have been observed to respond to species such as coatimundis (Rylands, 1981), tufted capuchins (Peres, 1993), and a variety of birds such as vultures, toucans and parrots (Heymann, 1990; Peres, 1993; Rylands, 1981) with anti-predator or defensive behaviour even though there are no known recorded instances of predation by these species. We have observed anecdotally that Wied's

marmosets (*Callithrix kuhli*), in the region of Rio de Janeiro, were actively chased by a channel-billed toucan (*Ramphastos vitellinus*). The marmoset group displayed fear behaviour and fled. Juvenile vervet monkeys have been found to make the mistake of giving raptor alarm calls also to storks and vultures, not just eagles, because these birds are of similar size and features (splayed wings) (Seyfarth & Cheney, 1980).

Several studies found, however, that captive-reared, predator-naïve primate test groups displayed anti-predator behaviour towards the predatory stimuli (Blumstein, Cooley, Winternitz, & Daniel, 2008; Griffin, Evans, & Blumstein, 2001). Hence, it has been theorised that relatively little predator experience may be required in order for a prey animal to recognise a potential threat visually as specific visual cues may be shared between predator groups (e.g., frontally placed eyes, short neck, pointed teeth), and that such cues of morphology are fairly consistent and reliable means of identification of predators (Blumstein, Daniel, Griffin, & Evans, 2000).

In contrast, the impact of acoustic cues on marmosets has not been well studied. Only two Platyrrhines have been tested for their ability to respond to and acoustically recognise aversive predator signals (Friant, Campbell, & Snowdon, 2008; Searcy & Caine, 2003) and, across primates species generally, only twelve species so far have been tested specifically for responses to acoustic predator signals (see Blumstein et al., 2008 for review; for additional species see Arnold & Zuberbühler, 2006; Friant et al., 2008; Yorzinski, & Ziegler, 2007).

Although predators may be silent while hunting, they may and do vocalise at other times and, on occasion, might vocalise when hunting. At the very least, a predator's vocal behaviour indicates its presence and may increase vigilance in the prey species (Blumstein et al., 2000, 2008), and thus one would expect that auditory signals are not unimportant. There is evidence from a variety of prey species that auditory cues of a potential predator alone elicit anti-predator behaviour and alter the behaviour of the prey animal in other ways, such as reduced foraging (Searcy & Caine, 2003). Some birds of prey are known to use vocalisations to flush their prey from cover (Smith, 1969). Predation on common marmosets by one of these raptor species, *Micrastur semitorquatus*, has been observed (Alonso & Langguth, 1989). The recognition of these calls could aid in forewarning primates to avoid predation (Macedonia & Yount, 1991). Other raptors, such as the harpy eagle (*Harpia harpyja*), a suspected predator of marmosets, have also been observed vocalising prior to attacking prey (Gil-da-Costa, Palleroni, Hauser, Touchton, & Kelley, 2003). It has also been shown that some primates do respond to the vocalisations of leopards (e.g., Zuberbühler, 2000, 2001) despite leopards being silent, ambush predators. Auditory cues may also be particularly important in environments in which visual range is limited (Khayutin, 1985). Indeed, Searcy and Caine (2003) found that captive Geoffroy's marmosets showed stronger anti-predator behaviour when played the vocalisation of a red-tailed hawk (*Buteo jamaicensis*) than to a raven (*Corvus corax*) or the recording of a power drill. The marmosets were observed to display alarm calling, startle reactions, freezing and hiding in response to the predator vocalisations. The authors suggest that marmosets may use auditory cues associated with specific

predators as early warning signals that a predator is in the vicinity (Searcy & Caine, 2003). Therefore, it was important in our study to include predatory vocalisations as a potential aversive stimulus on captive marmosets.

In this paper, we report data on responses to visual and auditory aversive cues presented separately and together. We used as many males as females in age groups ranging from two to 13 years, including related and unrelated individuals. This sample allowed us also to analyse whether or not sex, kinship or age difference played a role, or whether individuals responded differently. We know that sex and age differences have been found in some primate species in their response to particular stimuli and situations, such as exploration of novel stimuli and environments or in task completion (e.g., Buirski, Plutchik, & Kellerman, 1978; Fragaszy & Mason, 1978; Gursky, 2005; Mendoza, Lyons, & Saltzman, 1991; Yamamoto, Domeniconi, & Box, 2004). Sex differences have also been found in the anti-predator strategies of some primate species (e.g., Ouattara, Lemasson, & Zuberbühler, 2009), but not in others (e.g., Hirsch, 2002). Genetic features aside, this paper also explores behavioural differences at the level of individual responses. Individual variation has often been simply interpreted as biologically meaningful, but non-adaptive, variation around an adaptive mean (Wilson, 1998). This is surprising as stochastic variations in the behaviour and physiology of individuals are a fundamental requirement for Darwin's theory of evolution (Itoh, 2002) and were identified as having an influence on adaptation of different populations to local conditions of the same species (Dall, Houston, & McNamara, 2004). Wilson (1998) suggested that natural selection needed to encompass adaptive individual differences within single populations. Indeed, a large number of studies now supports the theory that individuals differ in suites of correlated behavioural traits, such as temperament (e.g., Bell & Stamps, 2004; Drent, van Oers, & van Noordwijk, 2003; Iguchi, Matsubara, & Hakoyama, 2001; Schuett & Dall, 2009; Sih, Bell, & Johnson, 2003; Wilson, 1998).

Individual differences in group-living species are of particular interest in establishing how diversity in behaviour and skills might be useful for the group as a whole. For instance, multiple membership can increase vigilance time per group, but minimise the amount of time the individual must remain vigilant, improving the chance that a predator will be detected (Elgar, 1989; Lima & Zollner, 1996). Some studies suggest that 'boldness' in anti-predator behaviour is linked to increased mating success (e.g., Godin & Dugatkin, 1996; Hedrick, 2000) and to fewer attacks and deaths in encounters with predators (e.g., Godin & Davis, 1995). Presumably, caution has as much a place in a group as boldness and, under certain circumstances, may save lives.

We hypothesised and tested experimentally that marmosets at the University of New England might show some role division in fight and flight responses. We further predicted that the combination of visual and auditory stimuli, when presented to the marmosets simultaneously, would enhance anti-predator responses, based on the threat-sensitivity predator avoidance hypothesis (Helfman, 1989) and possibly even multimodal signalling theory (Partan & Marler, 1999).

Method

Subjects and Housing

The marmosets were housed at the University of New England in Armidale, New South Wales, Australia (see Kaplan & Rogers, 1999, 2006 for further details). The captive-born, twelve adult marmosets (six males, six females) participating in this study were matched by age and sex. They ranged in age from 29 to 167 months with a mean age ($M \pm SE$) of 70 months (± 13.02). The ages of males and females were not significantly different (two-tailed, Mann-Whitney U-test, $z = -0.482$, $p = 0.63$).

The marmosets were housed in same-sex groups of related individuals, except for two individuals that were housed alone due to social aggression. Home cages (mean cage space 3.85 m^3 per marmoset) were connected to indoor rooms ($4.0 \times 4.0 \times 3.5 \text{ m}$) and outdoor cages ($1.7 \times 1.7 \times 2.6 \text{ m}$) via runways. Enclosures were furnished with hessian-covered climbing structures, including branches, tunnels, rope, chain and dowel. The outdoor cages were located in an enclosed space with open-spaced brick walls that allowed light and some weather elements to pass through, but reduced visibility. Overhead viewing was blocked by an overhang. Although birds of prey occasionally flew overhead they could not be seen from the outdoor cages by the marmosets and had not been heard vocalising in the vicinity of the marmoset housing. It can therefore be assumed that this captive, and captive-born, group of marmosets was predator naïve.

The home rooms and indoor rooms were temperature controlled between 18°C and 30°C , and had a day-night cycle of 12 hr:12 hr (07:00 hr - 19:00 hr light period). The outdoor cages received sunlight, and ultraviolet lights (350 – 390 nm) in the home rooms were turned on for 30 min per day. The marmosets were fed once daily between 12:00 hr and 14:00 hr with sufficient food to last for a 24-hr period. The diet varied daily and included meatloaf, polenta cake, a range of fruit and vegetables, yoghurt, peanuts, cereal, dog pellets and vitamin supplements. Water was provided *ad libitum* in each cage and the play rooms to which the marmosets had access.

Stimuli

The study on anti-predator responses is part of a larger study on responses to different sensory modalities in marmosets and the behavioural choices they make on presentation of different stimuli (negative, positive and neutral) in different sensory modalities. Here we report the specific study of anti-predator responses to auditory and visually aversive stimuli. Given that the marmosets were predator-naïve, an extensive set of preliminary trials sought to establish first to which visual and auditory stimuli the marmosets responded most and least aversively. In these preliminary trials, 4 visual potential predatory stimuli were presented. Results showed that the most consistently aversive stimulus was a taxidermic specimen of a spotted quoll (*Dasyurus maculatus*), a relatively small, native Australian mammal, but larger than marmosets (on average 60 cm long, excluding the tail, and 1.3 kg; in contrast common marmosets are on average 16 cm long, excluding the tail, and 0.4 kg) that the marmosets would never have seen before. The quoll is indeed a carnivore and resembles in type a small feline, similar to a margay, thought to be a natural predator of marmosets (Passamani, 1995). This model reliably elicited mobbing behaviour by all marmosets. Preliminary trials established that the marmosets did not habituate to this stimulus as, indeed, would be expected if a stimulus was considered dangerous and predatory (no significant difference in the number of mobbing vocalisations across three testing periods over two years; $F = 0.345$, $df = 2$, $p = 0.711$). Earlier studies in our laboratory (Pines, Kaplan, & Rogers, 2005) had found that the same individuals habituated readily and dramatically to novel, but innocuous, objects (reduced response after 1 day exposure to no response within three testing days). Auditory stimuli were trialled using the sounds of seven different predator vocalisations. The auditory stimulus that most clearly startled the marmosets, and did so consistently, was a recording of leopard growls. The marmosets displayed fear behaviour, including freezing, trembling and hiding. The growls chosen were played back to the marmosets at 60 dB and the sequence was created from a collection of audio clips (junglewalk.com). Innocuous visual and auditory stimuli were also presented as controls in each trial (an unattached PVC tube placed in the room, previously seen by the marmosets as part of climbing structures, was used in trials with visual presentations and, for the trials involving auditory presentations, we used background noise recorded

near the marmosets' building). We found significant differences in the behaviour of the marmosets between the aversive and control stimuli (mobbing vocalisations and fear responses were at or close to 0 towards the control stimuli), while responses to aversive stimuli of any kind were high and remained so consistently. Hence, the act of the experimenter placing an object in the room per se was not the reason for their response and could be ruled out as a variable.

Working with captive and predator-naïve primates raised the question of ecological validity. Clearly, quolls do not occur in the marmosets' natural environment and leopard growls were as unfamiliar to the marmosets as any other predatory sounds played back to them would have been. Hence, it was not the point to establish authenticity of predators of marmosets in the wild but, instead, to find stimuli that would elicit consistently aversive responses of the kind that might be displayed in predatory situations. As such, both stimuli fulfilled the criteria of responses to an aversive/predatory stimulus that one would expect in an ecologically authentic context.

In the experiment, only one auditory and one visual stimulus were used and these were the ones that had shown the highest arousal and highest and most consistent response rate in the marmosets, in this case, the taxidermic model of a quoll and the leopard growls. These stimuli were then used in individual presentations or in combination to one marmoset at a time. When the auditory stimulus was combined with the visual stimulus, the visual stimulus first remained covered and was placed within arm's reach of the door to the testing room and placed on a table. On removal of the cover from the quoll the auditory stimulus was played so that the marmosets experienced both stimuli simultaneously.

The combined presentation of auditory and visual stimuli was an artefact in so far as the two would not occur together naturally in a predatory situation, as most predators are silent when they hunt. However, the threat-sensitivity predator avoidance hypothesis argues that the association and simultaneous combination of two or more aversive stimuli in different sensory modalities should increase the response (Helfman, 1989), while other researchers have pointed out that such combinations might alter the response altogether (Partan & Marler, 1999; Stein & Meredith, 1993). Having established in pre-trials (as mentioned previously) that one stimulus had invoked fear (auditory stimulus) and the other (visual stimulus) mobbing calls (i.e., two different affective states), it could not be presumed that response intensity would simply increase when both were presented simultaneously.

Experimental Procedure

All experimental procedures were approved by the University of New England Animal Ethics Committee and are in accordance with the *Australian Code of Practice for the Care and Use of Animals for Scientific Purposes edition 7* (Australian Government; National Health and Medical Research Council, 2004).

Experiments were conducted between 9:00 hr and 12:00 hr in the indoor rooms. No transport or stress-inducing transfers to a testing arena preceded trials. The indoor room as well as the outdoor cages were connected to the home room by a number of runways, containing removable divider partitions in sections of equal length. When these were removed between home room and indoor room, individual marmosets either freely followed the removed partitions or were readily coaxed from their home cage (and cage mates) using food rewards placed behind partitions before their removal. Access back to their cage was blocked during trials using the same divider partitions in the runways. The marmosets have been accustomed to this procedure over years of testing. During testing, the marmosets had access to the entire large indoor room, including vertical, horizontal and diagonal climbing structures. Enrichment objects and furnishings were kept identical for the period of the trials except for the changes made on the presentation area of stimuli. Marmosets were observed and filmed through a one-way mirror.

Each marmoset was tested individually for several reasons: it was important to record and be able to identify individual vocalisations during analysis, to ensure that the behaviour of the marmoset remained uninfluenced by conspecifics, and that the attention of the marmoset was focused on the stimulus being presented.

The visual stimulus was covered and then placed on a table inside the room but within the experimenter's reach from the door. A zippered canvas screen attached between the edge of the door and the door frame prevented the marmosets from seeing the experimenter during the placement and

removal of the stimulus. The testing period began upon removal of the cover from the visual stimulus. The visual stimulus was placed on a platform (294 cm x 60 cm, 75 cm from the ground), with the nose of the taxidermic carnivore 10 cm from the edge closest to the branches. The auditory stimulus was played through a speaker (Logitech Z-5, USB digital) at 60 dB from the front of the room at table level, placed just behind the table, attached to a computer (HP Pavillion dv9000) outside the room.

Visual and auditory stimuli were presented individually first, before the marmosets were exposed to the combination of the two sensory modalities. Behaviour was observed from a position behind the one-way mirror and scored from the playback of the video recordings. Vocalisations were recorded using a digital audio recorder (Marantz, solid state recorder PMD670, gain 10, microphone: Sennheiser MKH 418S P48). The vocalisation recordings were converted to sonograms, and the calls identified, using Adobe Audition version 3.0.

Period of Observation

The stimuli were presented on different days to each marmoset so that no individual was tested more than once per day, with a minimum of one day between stimulus presentations. Two trials were conducted for the individual presentations of visual and auditory stimuli to determine if the behavioural response of the marmosets to these stimuli was consistent. The marmosets were observed individually for 1 min in the presence of these stimuli. This period of time was selected based on attention span of marmosets. Previous studies had shown that interest and attention towards stimuli waned after the first minute (Brown, Kaplan, Rogers, & Vallortigara, 2009). Although response rate might have been maintained for a longer time span given the aversive nature of the stimuli, 2 min pre-trials showed little behavioural difference between 1 and 2 min exposure. Hence, there was no need to expose the animals to the fearful stimuli for more than a minute. Moreover, we were testing the immediate behavioural responses to the stimuli and this purpose was well served by the 1 min exposure.

Behaviour Scored

Scoring began when the visual stimulus was revealed and/or the auditory stimulus played. Behaviour scored included latency to vocalise, latency to approach (visual stimuli only) and total number of vocalisations elicited during presentation of stimuli. Latency to approach or to vocalise was timed in seconds to the nearest 2 ms. A marmoset was considered to have approached when it had moved directly towards the stimulus, decreasing the distance between itself and the stimulus by at least 50 cm from the marmoset's original position. All vocalisations were recorded for later analysis. Research results of other projects had shown that call types are very varied and call combinations were not necessarily stereotyped (Stewart, 2009). It was therefore important to be able to compare whether certain stimuli elicited more call types and different combinations of vocalisations than others. In addition, the distance of the marmoset from the visual and/or visual with auditory stimuli was recorded every 5 s. Preliminary testing had shown that the marmosets gave no indication of recognising the speaker as the point of origin for the auditory stimulus, in terms of either their approach/withdrawal movement or their head orientation.

Distance was measured as the distance of the marmoset from the visual stimulus on the platform at interval sampling of every 5 s within the first 60 s of exposure (13 data points). The area adjacent to the predator model was subdivided into several zones, as is common practice in similar research on fish (Brown, Golub, & Plata, 2001). There were three zones identified: the inner zone was a distance close enough to be within striking distance of the predator (high risk zone) and around the face/mouth of the predator is, in the fish literature at least, identified as the attack cone avoidance area (George, 1960).

This zone extended from 0 to 100 cm (if marmosets perched on branches of eye height of the predator or below) or stepped onto the platform. The distance of 100-150 cm was a middle zone, close but outside striking distance, and the third zone any distance greater than 150 cm or well above eye height in a branch above (but more than 150 cm) of the taxidermic model. These zones enabled us to then classify marmosets by distance and zone. All marmosets seen at any time within this high danger zone were later classified as Group A. Individuals remaining at distances greater than 150 cm (well outside the striking distance) were classified as Group B if they also did not once come within

100 cm of the quoll. These categorisations were used for both the visual stimulus on its own and the visual-auditory combination. The auditory measure was purposely not considered and analysed in terms of distances. Although a speaker offered a concrete local point of identification, the sound was reflected from the walls in all directions and a measure of distance to the stimulus was not considered accurate. From pre trials we found that the marmosets showed no apparent behavioural indication that they identified the speaker as the origin of the sound.

As it may be argued that marmosets who occupy a greater distance from the model predator may have no interest in the aversive stimulus, rather than be simply avoiding a risk zone, we also presented the marmosets, in a separate trial, with a small piece of a favourite food item (marshmallow) and placed it closely beside the predator model, i.e., with potential striking distance (20 cm). In pre trials we had established that all marmosets were very quick to retrieve a marshmallow (100% retrieval rate), when presented to them on its own. By creating a conflict between a desirable visual object and a predatory one, we were able to test the relative strength of the two opposing affective states within the same visual modality. This also allowed us to test whether some marmosets would approach regardless of risk or exercise constraint and not retrieve the favourite food item.

Statistical Analysis

Statistical analyses were performed using SPSS (SPSS Inc. Release 17.0.0). Normality and equal variance (Levene's test) were assessed. The two trials conducted for the individually presented visual and auditory stimuli and minute comparisons of the combined stimuli presentation were analysed across all behaviours using paired t-tests for normal data and Wilcoxon signed rank tests for non-normal data when transformation was unsuccessful. Age correlations were conducted using either Spearman's or Pearson's test, depending on whether the data was normal. Sex differences and Group A versus Group B marmosets were tested for using a multivariate general linear model with *post hoc* Tukey's tests conducted. Bonferroni adjustments were made for each stimulus, based on the number of behaviours analysed. Although there was only one observer recording the described behaviours, an inter-observer reliability test was conducted and this showed reliability exceeding 95%.

Results

We tested the hypothesis that sex and age differences played a role in the behavioural response of common marmosets to predatory stimuli. No significant sex or age differences were found in any of the types of behaviour measured in response to presenting the visual and auditory stimuli alone or in combination. Paired t-tests and Wilcoxon signed ranks tests revealed no significant difference between the trials for the visual and auditory stimuli for any of the behaviour measured. Hence, the two trials were combined and the mean used for all further analysis. These tests also found no significant difference between minute one and minute two of the combined stimulus presentation for mean distance, closest distance or the number of vocalisations. The first minute was therefore used in the behavioural analyses and for comparisons with the results of the stimuli presented alone. If latency to approach or vocalise was longer than 60 s during the presentation of the combination for any individual, it was recorded as being 60 s.

Presentation of Visual Stimulus

Movement behavior. Based on the risk-taking criteria described in the methodology, five of the 12 marmosets were classified as Group A (three males, two females) and five as Group B (three males, two females) (Table 1). Marmosets that spent the majority of their time between these distances (100 – 150 cm) were

classified as middle-ground animals, showing neither a strong degree of cautiousness nor any indication of physical risk-taking. The scores of marmosets that fitted neither category easily (two individuals) were further analysed for total number of vocalisations, latency to approach and latency to vocalise and then a category determined. Two marmosets occupied a middle range, at least in terms of distance. Although all marmosets retrieved the food item when it was presented individually, we found that five marmosets did not do so while the taxidermic model was nearby. Three of the five individuals (one male, three females) were from Group B, one (female) was from Group A and the other (female) was from neither group. In addition, both groups consisted of members from different families, rooms or cages (Table 1).

Table 1

The relatedness of individuals, either through family grouping, room grouping and cage grouping, and their classification as either Group A or Group B for the visual stimulus alone, or the visual-auditory stimulus combination (A = adult, F = female, M = male).

Individual	Family group	Room	Cage	Visual stimulus	Visual-auditory stimulus
AF1	3	2	5	Group B	Group B'
AF2	1	1	2	Group B	Group A'
AF3	2	3	7	Group A	Group B'
AF4	1	1	1	Group B	-
AF5	1	1	2	-	-
AF6	1	1	1	Group A	Group A'
AM1	1	3	6	Group A	Group A'
AM2	2	2	4	-	Group B'
AM3	1	3	6	Group B	Group B'
AM4	2	2	4	Group B	Group A'
AM5	1	3	8	Group A	Group B'
AM6	1	3	8	Group A	Group A'

The mean distance of marmosets in Group A from the quoll (117.58 cm \pm 6.54 cm standard error) was significantly different from that of marmosets in Group B (172.96 cm \pm 7.07 cm) ($F(1, 11) = 33.096, p = 0.0001$). Their mean distance over time in relation to the visual stimulus is shown in Figure 1. The closest distance of approach was also significantly different between the two groups ($F(1, 11) = 13.207, p = 0.007$), Group A individuals having a mean approach distance of 88.2 cm (\pm 2.46 cm) and Group B marmosets approaching to a mean distance of 130.8 cm (\pm 11.46 cm). The mean latency to approach the visual stimulus at least 50 cm from the a marmoset's starting point was 14.96 s (\pm 2.42 s) for Group A and 19.02 s (\pm 3.2 s) for Group B individuals. This was not significantly different ($F(1, 11) = 1.027, p = 0.341$).

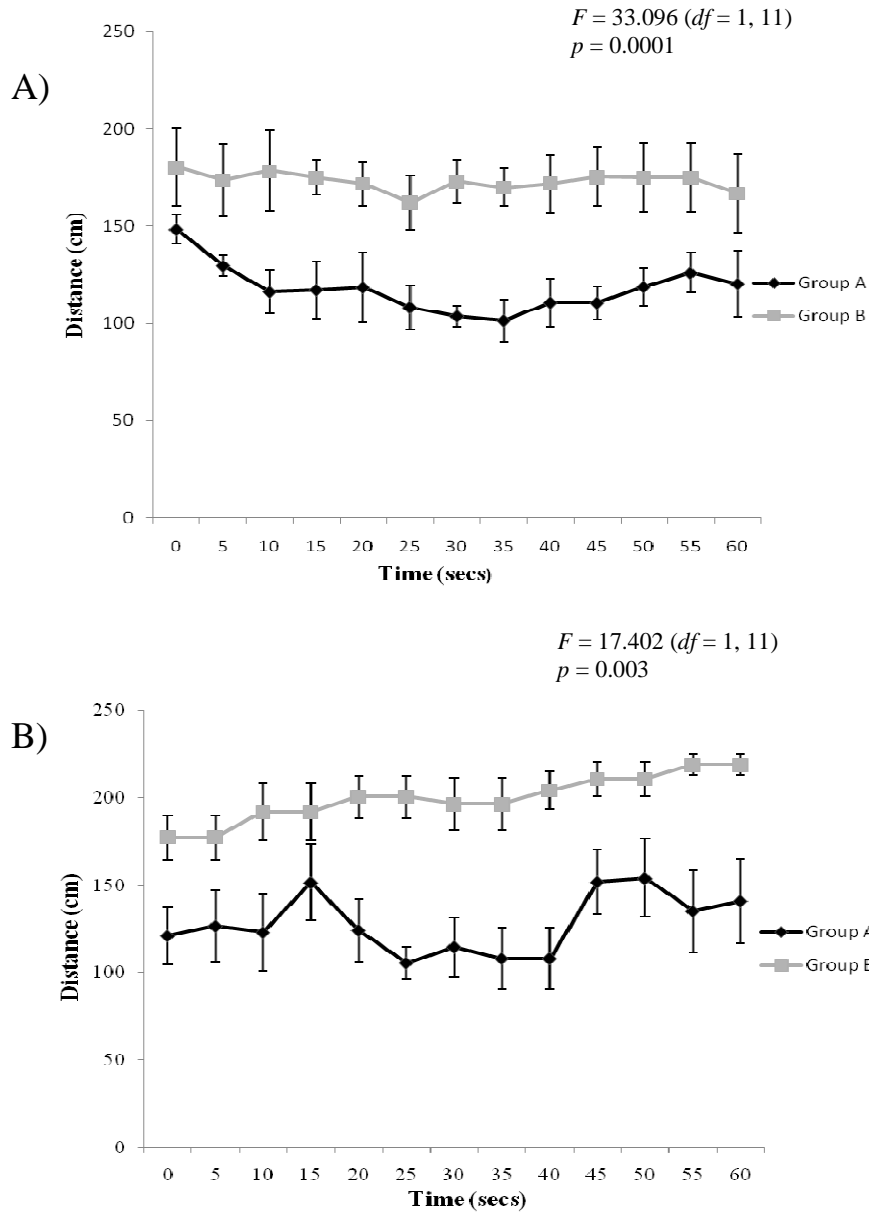


Figure 1. Mean distance (cm) over time (60 s) of Groups A and B during the presentation of the visual stimulus alone (A), and Groups A' and B' during the presentation of the combined visual-auditory stimulus (B).

Vocal behavior. Group A and B individuals were also significantly different in the total number of vocalisations given on presentation of the quoll ($F(1, 11) = 6.832$, $p = 0.031$). Group B marmosets made fewer vocalisations (mean of 26 ± 7.49 vocalisations per marmoset) than Group A marmosets ($M = 57.3 \pm 9.35$ vocalisations per marmoset). The majority of vocalisations given by the marmosets were mobbing calls, primarily tsik and crackle vocalisations (Epple,

1968) (Fig. 2). No significant differences were found between Group A marmosets and Group B marmosets for these vocalisations; tsik ($F(1, 11) = 4.35, p = 0.07$), crackle ($F(1, 11) = 3.986, p = 0.081$). The mean latency to vocalise was 5.06 s (± 3.31 s) for Group A and 10.41 s (± 5.84 s) for Group B marmosets; there was no significant difference between these means ($F(1, 11) = 0.634, p = 0.449$).

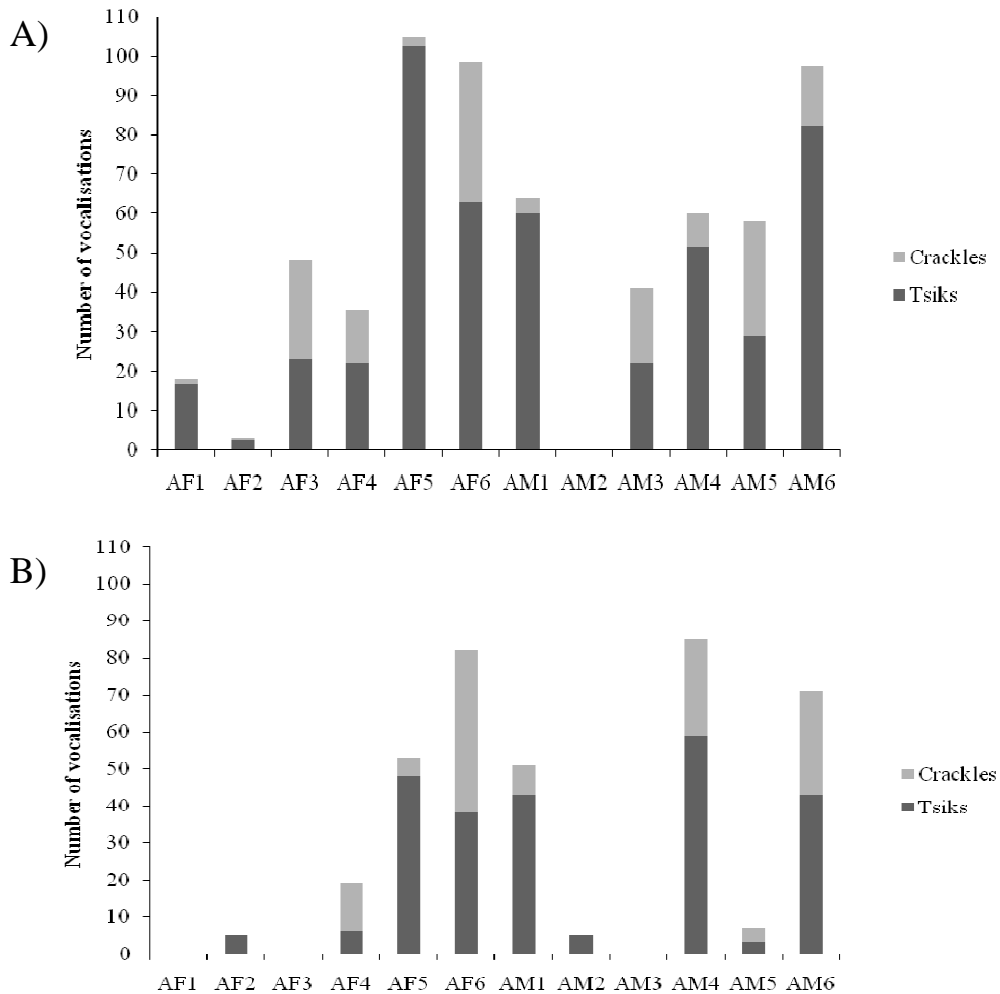


Figure 2. Mean number of mobbing vocalisations (tsiks and crackles) given by each individual in response to A) visual predator model alone, and B) visual-auditory combination stimulus.

A correlation was found between the mean distance to the model predator and the number of vocalisations elicited ($R^2 = 0.648, p = 0.005$) (Fig. 3). Marmosets venturing close to the model (i.e., Group A) produced more vocalisations, predominantly mobbing calls.

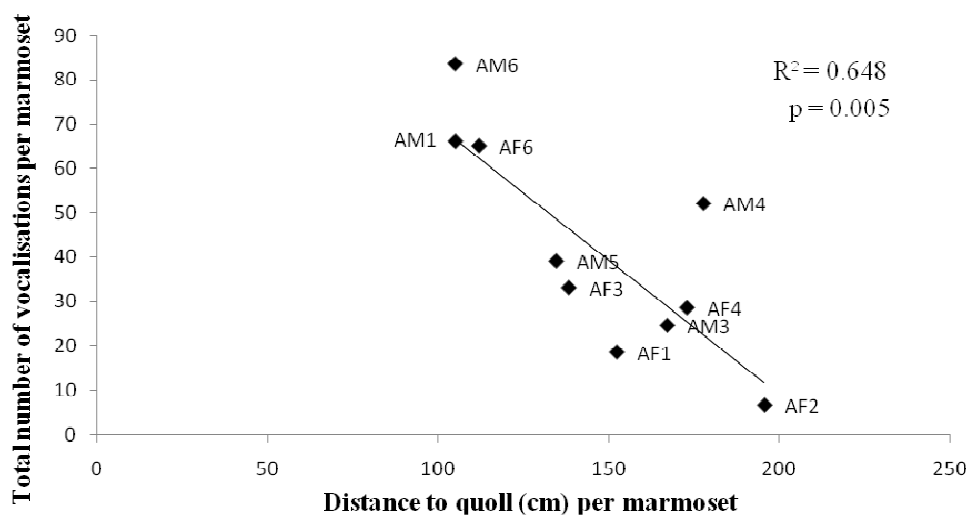


Figure 3. Correlation between mean distance from quoll (cm) and mean number of total vocalisations per marmoset (Group A and B individuals) during the presentation of the visual stimulus alone.

Presentation of Auditory Stimulus

The mean latency to vocalise during the auditory stimulus presentation across all 12 marmosets was 38.25 s (± 4.98 s) with a mean of 4.83 vocalisations (± 3.16) given during the 60 s testing period. The majority of these vocalisations were contact calls, such as the ‘phee’ (Epple, 1968), which is a long-distance contact vocalisation, but occurred at too low a frequency to analyse separately. One individual, AF2, vocalised considerably more than the other marmosets, occurring predominantly in the first trial of the auditory stimulus.

Results from the presentation of the auditory stimulus were compared with those of the visual stimulus (i.e., as per Groups A and B individuals). No significant difference was found between these two groups in either latency to vocalise ($F(1, 11) = 0.354, p = 0.568$) or the total number of vocalisations ($F(1, 11) = 1.465, p = 0.261$) in response to the auditory stimulus. No other combination of individuals to form groups was evident.

Comparison of Singular Visual and Auditory Presentations

A comparison of the latency to vocalise and total number of vocalisations made when visual and auditory stimuli, using the scores of all 12 marmosets, revealed that both the total number of vocalisations ($t = 4.616, p = 0.001$) and the latency to vocalise differed significantly between the conditions ($t = -4.94, p = 0.0001$). They made significantly fewer vocalisations and had a longer latency to vocalise on presentation of the auditory stimulus compared to presentation of the visual stimulus.

Visual-Auditory Combination

The five types of behaviour scored (mean distance, closest distance, latency to vocalise, latency to approach and total number of vocalisations per individual) were analysed using the Group A and Group B marmosets as identified from the presentation of the visual stimulus alone. No significant difference was found between these two groups for any of the behaviours recorded to the visual-auditory stimulus ($F(1, 11) = 2.474, p = 0.2$).

Movement behavior. The presentation of the combined auditory and visual stimuli produced some behavioural changes in the distance and movement patterns of the marmosets (Table 1). Three of the five marmosets (two males, one female) that had approached the taxidermic model within striking distance when it was presented singularly, did so again when the combined visual and auditory stimuli were presented (Group A'). The other two marmosets (one male, one female), that had belonged to Group B in the first set of trials, staying well away from the model predator, were now clearly foraging into the critical 100 cm zone. The male (AM4) approached within 100 cm several times, but was also observed at distances greater than 150 cm for the majority of the time recorded. As AM4's vocalisation levels matched those of other Group A' classified marmosets, with a low latency to vocalise and approach during the combination stimulus presentation, he was classified as Group A'.

While two of the five marmosets (one male, one female) from the original Group B remained further away in the combined presentation of visual and auditory stimuli, two of the original Group A marmosets (one male, one female) and one male that had not been placed into either grouping now also remained further away (Group B'). Overall, five marmosets were again in Group A' (three of the original members) and five marmosets were in Group B' (two of the original members). As described, the composition had changed in both groups, indicating that the presentation of the combined stimuli had different effects on different individuals. Again, both groups were made up of individuals from different families, rooms or cages (Table 1).

The mean distance of Group A' from the quoll, during the combined visual-auditory presentations, was 138.45 cm (± 11.23 cm), whereas Group B' marmosets kept at significantly greater distance ($F(1, 11) = 17.402, p = 0.003$) of 199.65 cm (± 9.44 cm). The mean closest distance between the two groups was also significantly different ($F(1, 11) = 38.356, p < 0.001$). Group A' individuals approached to a mean distance of 84 cm (± 5.09 cm), whereas Group B' individuals had a mean approach distance of 173.2 cm (± 13.47 cm). The mean distance over time of the two groups is shown in Figure 1. The two groups also showed a significant difference in latency to approach ($F(1, 11) = 295.84, p = 0.0001$), none of the Group B' marmosets approaching the quoll during the presentation of the stimulus, whereas Group A' had a mean latency to approach of 13.07 s (± 6.22 s).

Vocal behavior. In response to the visual-auditory combination, Group A' marmosets gave significantly more vocalisations ($F(1, 11) = 18.199, p = 0.003$) with a mean number of 41.4 (± 9.05) vocalisations than Group B' marmosets,

(mean of 2.6 (\pm 0.93) times). The majority of these vocalisations were mobbing calls, particularly tsiks ($F(1, 11) = 16.196, p = 0.004$) and crackles ($F(1, 11) = 6.791, p = 0.031$) (Fig. 2). There was a significant difference in the latency to vocalise between the two groups ($F(1, 11) = 27.945, p = 0.001$). Group A' had a shorter latency to vocalise than Group B', with means of 2.78 (\pm 1.6 s) and 46.83 (\pm 8.18 s) seconds, respectively.

Comparison Between Stimuli, Presented Alone and in Combination

A multivariate general linear model analysis determined that there was no significant difference between Groups A' and B' for the five types of behaviour analysed on presentation of the visual predator model on its own ($F(1, 11) = 2.251, p = 0.226$) or for the two types of behaviours analysed for the leopard vocalisation on its own ($F(1, 11) = 2.671, p = 0.137$).

Comparisons of behaviour to the different stimuli were made using all 12 marmosets. The marmosets came significantly closer during the presentation of the visual stimulus alone than during the visual-auditory combination ($t = -2.155, p = 0.05$). A significant difference between the response to the visual stimulus alone and the visual-auditory combination was also found for the latency to approach ($t = -2.745, p = 0.019$). The latency to vocalise during the presentation of the visual-auditory combination was significantly shorter than when the auditory stimulus was presented alone ($t = -2.273, p = 0.044$), but not when the visual stimulus was presented alone ($t = -1.62, p = 0.134$). The total number of vocalisations made during presentation of the visual-auditory combination was significantly lower from the number of vocalisations made during presentation of both the visual ($t = -3.721, p = 0.003$) and higher than when the auditory ($Z = 2.798, p = 0.017$) stimuli was presented alone.

Mann-Whitney U tests were used to compare the eight individuals of the one family group to the other four marmosets, unrelated to the eight, to determine if kinship affected the behaviour of the marmosets in response to the stimuli. No significant differences were found between the two kinship groups for the visual stimulus alone; mean distance ($p = 0.497$), closest distance ($p = 0.799$), latency to approach ($p = 0.126$), latency to vocalise ($p = 0.159$) and total number of vocalisations ($p = 0.174$). No significant differences were found between the two kinship groups for the auditory stimulus alone; latency to vocalise ($p = 0.932$) and total number of vocalisations ($p = 0.794$). No significant differences were found between the two kinship groups for the combined visual and auditory stimuli; mean distance ($p = 0.171$), closest distance ($p = 0.552$), latency to approach ($p = 0.319$), latency to vocalise ($p = 0.544$) and total number of vocalisations ($p = 0.394$).

Discussion

Contrary to our predictions no sex or age differences were found. Response patterns were also checked against and compared with kinship or room/cage affiliations. We found no significant evidence of such patterns. Individuals that had dared to approach within striking distance of the taxidermic model were not

particularly affiliated with each other, either through kinship, or as room or cage mates, and no other patterns of pointing to similarities as a result of affiliation or shared experience could be detected. Indeed, it could be argued that awareness of aversive stimuli and vigilance ought to be well developed in all adult individuals.

These findings suggest that other factors, such as temperament or personality traits, may have shaped the responses, as has also been found in other primate studies (e.g., Box, 1982; Clarke & Boinski, 1995; Weinstein & Capitanio, 2008). Indeed, our results point to individual differences and, in the context of our experiments involving aversive, if not predatory, stimuli, risk-taking and risk avoidance (or cautiousness) would appear to be useful criteria for identifying Group A and Group B individuals. There is ample evidence in research on fish behaviour that some individuals take risks in the form of predator inspection while others stay away, although even those inspecting predators keep a certain minimal distance and avoid one part of the predator's body more than others, usually the predator's head region (Brown & Dreier, 2002; George, 1960).

Arguably, the greatest risk for a prey animal is to get within striking range of a potential predator. Our data showed that close proximity to the visual stimulus (risk-taking) was found to correlate with other behaviour recorded in the same tests, viz. latency to approach, closest approach and number of vocalisations. This correlation between proximity (with short latency to approach) and mobbing vocalisations (see Fig. 3), suggests that the behavioural sequence was not due merely to curiosity. The display of a suite of behaviour matched that of mobbing behaviour rather than that of quiet investigative and curious inspection. Despite the risk, predator mobbers may benefit conspecifics by gaining additional and important information about the level of predation risk (Lima & Dill, 1990; Magurran & Girling, 1986; Pitcher, Green, & Magurran, 1986).

By contrast, the behaviour of those marmosets staying consistently far away from the taxidermic model (see Fig. 1) might be interpreted either as risk avoidance or as a lack of interest in the stimulus. Had the latter been the case, they should not have hesitated to approach and retrieve a favourite food item placed on the table despite the presence of the taxidermic model. The evidence speaks against this interpretation. Three of the five marmosets (Group B) did not retrieve the food at all, but had done so when it was presented on its own it before and, in that trial, had shown no difference in latency to retrieve the food in comparison to the other marmosets (Group A). On those grounds, it would appear that these three marmosets associated some risk with the visual predator model. The two marmosets (Group B) that did retrieve the food were individuals AF2 and AM3. AF2 had been ranked as a cautious marmoset based on the response when presented with the visual predator model alone. While AF2's latency to retrieve the food in the presence of the model predator was the lowest recorded it is important to note that, AF2 swiftly moved into the branches provided, well away from the model, and hence the food was not consumed near the predator model. AM3 who eventually took the food item, as AF2 had done, by contrast, waited for almost the entire trial period before acting. Just as AF2, AM3 then quickly snatched the food and returned to the branches to consume it, and did not remain in the near vicinity of the predator model either. The behaviour of AM3 in response to the two

predatory stimuli remained consistently cautious throughout the study. It cannot be concluded that Group B marmosets as a whole were indifferent to the visual predator stimulus, but perhaps one individual, AF2, did not perceive a high level of risk associated with this stimulus. Context and motivation may be factors influencing risk-taking by any individual, regardless of its general temperament.

Saying so, however, would imply that marmosets simply fall into two groups - cautious and risk-taking animals - and the idea of individual differences would indeed not be very robust. However, situational context changed the composition of individuals in each of these two groups across different tasks and suggested the adoption of different behavioural strategies and risk assessments by individuals according to circumstances. While some individuals that had been risk-takers when facing the visual stimulus alone became wary in response to the combined stimuli (visual and auditory), other individuals showed the opposite trend (see Table 1). There was also no direct relation of these categories to the expression of behaviour in tests with the auditory stimulus alone. Indeed, experience may have factored into the changed behavioural type of some marmosets when presented with the visual-auditory combination. Experience has been found to contribute to the response of individuals to certain situations, resulting in an observed change from a bold to shy classification, or vice versa (Frost, Winrow-Giffen, Ashley, & Sneddon, 2007).

The modality of stimulus presentation had a significant effect on all marmosets regardless of their tendency to come close or stay away when the stimuli were presented individually. When leopard vocalisations were added to the presentation, the mean results for the 12 marmosets showed a significantly longer latency to approach the visual stimulus and the mean distance was greater than in individual presentation of the visual stimulus. Other studies have shown that those individuals known to approach predators within populations differ in their minimum approach distance and in their tendency to inspect (Godin & Crossman, 1994; Magurran, 1986; Murphy & Pitcher, 1991). We found that marmosets showed strong differences in their approach patterns, especially to the visual-auditory stimulus combination, with AF2 getting as close as 68 cm while, in contrast, the closest approach of AM3 was as far away as 220 cm, keeping just about as great a distance as the room permitted. The individual differences presented here, and in previous studies, may be a reflection of differences in internal state and physical condition (Godin & Davis, 1995). These results suggest that cautiousness and risk-taking may be context-dependent. Coleman and Wilson (1998) proposed that 'shyness' and 'boldness' for any given situation may be interchangeable, with other factors playing a role between similar events. Approaching and mobbing a predator is a potential risk as it places an individual within close range of danger whilst also drawing attention to the individual. However, in doing so the individual is also informing the predator it has been spotted and that, as many predators of marmosets are ambush predators, any surprise attack will not succeed. Within a group-living species, individuals that put themselves at risk may also provide a benefit to the group as a whole (Box, 1999) and is not just a matter of individual temperament. If this were the case, one would

have expected consistent risk-taking across all stimuli by the same individuals with a corresponding increase in risk of being caught by a predator.

Individual differences were less obvious during the playback of the auditory stimulus (leopard vocalisation). Most marmosets vocalised little or not at all in response to the auditory stimulus and the mean latency to vocalise accounted for more than half the testing period. Indeed, all marmosets showed fear responses to the leopard vocalisation (freezing, fleeing and hiding behaviours) that they did not display when facing the visual model only, suggesting that they were not just responding to this stimulus as an aversive, potentially predatory, cue but also perceived the auditory cue by itself as qualitatively very different from the visual cue. These predator-avoidance behaviours have been noted in other studies testing the response of Callitrichids to other predator vocalisations (e.g., Friant et al., 2008; Searcy & Caine, 2003). Friant and colleagues (2008) also found that captive-bred tamarins respond to non-predator vocalisations with similar behaviours and suggested that it is the frequency of the sound that affects the behaviour and type of response of the recipient, as opposed to the prey animal recognising the potential predator. Leopards give a low frequency vocalisation, which has been theorised to be indicative of size (Owings & Morton, 1998; Peters & Tonkin-Leyhausen, 1999) and the marmosets may be responding to this cue within the stimulus. However, common marmosets have been noted to have reduced sensitivity to sounds around 4 kHz (Heffner, 2004); leopard vocalisations are typically below this frequency so their response appears to be more than just a factor of the perceived size of the animal making the vocalisations. Indeed, Friant and colleagues (2008) found that tamarins move to a higher location after hearing a jaguar vocalisation, which suggests that they perceive the vocalisations as not just coming from a large animal, but from a terrestrial predator.

The marmosets' strong differentiation between visual and auditory stimuli in our results is in agreement with Endler's (1993) suggestion that different sensory channels may be used to send different information when the signals are non-redundant (Partan & Marler, 1999). The behavioural response to the combined leopard growls and model carnivore suggested initially that the visual stimulus had a stronger influence on the reactions of the marmosets than the auditory stimulus alone. Based on the description of multimodal communication signals by Partan and Marler (1999, 2005), the combination of the visual and auditory predatory stimuli in this study should be classified as a non-redundant dominant signalling type, with the visual stimulus prevailing over the auditory.

However, the mean total number of vocalisations given to the visual-auditory combination was significantly different from both the stimuli when presented alone; fewer vocalisations were given to the combination stimuli than to the visual alone, but this was also more than given to the auditory stimulus alone. The combination of the two stimuli appeared to influence the response of the marmosets by altering how the stimuli were perceived and processed shown in the number of vocalisations given in each variation of presentation (see Fig. 2). This type of signalling is known as modulation, in which the combination of two signals known to elicit a particular behaviour individually also elicit that behaviour when presented together, but in an altered fashion (Partan & Marler, 1999).

It has been suggested that the increase in information from multiple cues allows animals to better assess their current risk of predation (Amo et al., 2004, 2006; Chivers, Mirza, Bryer, & Kiesecker, 2001; Hartman & Abrahams, 2000; Mathis & Vincent, 2000), thereby reducing the need for costly anti-predator behaviours in unnecessary situations. The addition of the vocalisation in response to the visual model of a predator may be an expression of a perceived increase in potential risk factor, as suggested by the threat-sensitivity predator avoidance hypothesis (Helfman, 1989). Indeed the marmosets remained significantly further away over the course of the trial period in the presentation of the visual-auditory combination than compared to the visual stimulus on its own. Importantly, individual behaviour towards the predator changed markedly according to visual or auditory presentation, alone or in combination. Such differences in response may tell us something about perceived thresholds of danger in different sensory modalities. That these show up as individual differences in some conditions does not detract from the fact that such differences in perception and responses may be useful to the group as a whole.

The marmosets in our study responded to the taxidermic model and the vocal playback of a leopard with the suite of anti-predator behaviour previously described in the literature (see Introduction) of marmosets studied in the natural environment and did so despite being captively-bred and predator naïve animals. They behaved towards the carnivorous quoll as if it were a potential threat and showed fear responses when hearing the low frequency of the leopard growl. While this is an interesting result in itself, our focus was on discovering whether aversive stimuli of different sensory modalities have an impact on how the response is shaped within a group of marmosets, and even within individuals. The results have shown clearly that auditory and visual aversive stimuli resulted in a different type or different strength of response. We suggest that auditory stimuli may play an important role in risk assessment in some situations and may be indicative of perception of increased risk level. Very clearly, the marmosets in this study responded spontaneously to the auditory stimulus with various expressions of fear, such as flight responses, trying to hide, trembling and even freezing. However, the resulting action to combined auditory/visual presentations or two visual (conflicting) stimuli was different among individuals, suggesting behavioural diversity and flexibility among the marmosets. Box (1999) had argued that such flexibility may be expressed in individual differences and may contribute to a sense of group stability. This may be through cautiousness to improve the likelihood of an individual's survival when faced with a predatory threat, an act that may also improve the chance of the survival of the group as a whole. Individual differences are thus perhaps not simply non-adaptive variations around an adaptive mean, as previously suggested (Wilson, 1998).

This project raised the question whether behavioural traits shown in one set of circumstances remain consistent within individuals across different situations. This will be further tested in our laboratory. However, one area that we were unable to test is the influence that related conspecifics and, in particular, dependent juveniles might have on the behaviour of individuals. It is conceivable that, as a

group, the perceived level of risk associated with the stimuli might be altered and hence lead to new outcomes.

References

- Alonso, C., & Langguth, A. (1989). Ecologia e comportamento de *Callithrix jacchus* (Primates: Callitrichidae) numa ilha de floresta Atlântica. *Review Nordest Biology*, 6, 105–137.
- Amo, L., Lopez, P., & Martin, J. (2006). Can wall lizards combine chemical and visual cues to discriminate predatory from non-predatory snakes inside refuges? *Ethology*, 112, 478-484.
- Amo, L., Lopez, P., & Martin, J. (2004). Wall lizards combine chemical and visual cues of ambush snake predators to avoid overestimating risk inside refuges. *Animal Behaviour*, 67, 647-653.
- Arnold, K., & Zuberbühler, K. (2006). The alarm-calling system of putty-nosed monkeys, *Cercopithecus nictitans martini*. *Animal Behaviour*, 72, 643-653.
- Australian Government; Natural Health & Medical Research Council (2004). *Australian Code of Practice for the Care and Use of Animals for Scientific Purposes edition 7*. Retrieved on the 23rd March 2008 from http://www.nhmrc.gov.au/files_nhmrc/file/publications/synapses/eal6.pdf.
- Barros, M., Boere, V., Huston, J. P., & Tomaz, C. (2000). Measuring fear and anxiety in the marmoset (*Callithrix penicillata*) with a novel predator confrontation model: effects of diazepam. *Behavioural Brain Research*, 108, 205-211.
- Barros, M., Boere, V., Mello, E. L., Jr., & Tomaz, C. (2002). Reactions to potential predators in captive-born marmosets (*Callithrix penicillata*). *International Journal of Primatology*, 23, 443-453.
- Bednekoff, P. A., & Lima, S. L. (1998). Randomness, chaos and confusion in the study of antipredator vigilance. *Trends in Ecology and Evolution*, 13, 284-287.
- Bell, A. M., & Stamps, J. A. (2004). Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, 68, 1339-1348.
- Bezerra, B. M., Barnett, A. A., Souto, A., & Jones, G. (2009). Predation by the tayra on the common marmoset and pale-throated three-toed sloth. *Journal of Ethology*, 27, 91-96.
- Blumstein, D. T., Cooley, L., Winternitz, J., & Daniel, J. C. (2008). Do yellow-bellied marmosets respond to predator vocalizations? *Behavioral Ecology and Sociobiology*, 62, 457-468.
- Blumstein, D. T., Daniel, J. C., Griffin, A. S., & Evans, C. S. (2000). Insular tammar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. *Behavioral Ecology*, 11, 528-535.
- Box, H. O. (1999). Temperament and socially mediated learning among primates. In H. O. Box & K. R. Gibson (Eds.), *Mammalian social learning: Comparative and ecological perspectives* (pp. 33-56). Cambridge, United Kingdom: Cambridge University Press.
- Box, H. O. (1982). Individual and intergroup differences in social behaviour among captive marmosets (*Callithrix jacchus*) and tamarins (*Saguinus mystax*). *Social Biology and Human Affairs*, 47, 49-68.
- Brown, G. E., & Dreier, V. M. (2002). Predator inspection behaviour and attack cone avoidance in a characin fish: The effects of predator diet and prey experience. *Animal Behaviour*, 63, 1175-1181.

- Brown, G. E., Golub, J. L., & Plata, D. L. (2001). Attack cone avoidance during predator inspection visits by wild finescale dace (*Phoxinus neogaeus*): The effects of predator diet. *Journal of Chemical Ecology*, *27*, 1657-1666.
- Brown J., Kaplan G., Rogers, L. J., & Vallortigara, G. (2009). Perception of biological motion by female but not male common marmosets. *Animal Cognition*, *13*, 555-564.
- Buirski, P., Plutchik, R., & Kellerman, H. (1978). A field study of emotions, dominance and social behavior in a group of baboons (*Papio anubis*). *Primates*, *14*, 67-78.
- Caine, N. G. (1998). Cutting costs in response to predatory threat by Geoffroy's marmosets (*Callithrix geoffroyi*). *American Journal of Primatology*, *46*, 187-196.
- Caine, N. G. (1993). Flexibility and co-operation as unifying themes in *Saguinus* social organization and behaviour: The role of predation pressures. In A. Rylands (Ed.), *Marmosets and tamarins: Systematic, behaviour and ecology* (pp. 200-219). Oxford, UK: Oxford University Press.
- Campbell, M. W., & Snowdon, C. T. (2009). Can auditory playback condition predator mobbing in captive-reared *Saguinus oedipus*? *International Journal of Primatology*, *30*, 93-102.
- Caro, T. (2005). *Antipredator defences in birds and mammals*. Chicago: University of Chicago Press.
- Cheney, D. L., & Wrangham, R. W. (1987). Predation. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. M. Wrangham, & T. T. Struhsakes (Eds.), *Primate societies* (pp. 227-239). Chicago: University of Chicago Press.
- Chivers, D. P., Mirza, R. S., Bryer, P. J., & Kiesecker, J. M. (2001). Threat-sensitive predator avoidance by slimy sculpins: Understanding the importance of visual versus chemical information. *Canadian Journal of Zoology*, *79*, 867-873.
- Clara, E., Tommasi, L., & Rogers, L. J. (2008). Social mobbing calls in common marmosets (*Callithrix jacchus*): Effects of experience and associated cortisol levels. *Animal Cognition*, *11*, 349-358.
- Clarke, A. S., & Boinski, S. (1995). Temperament in non-human primates. *American Journal of Primatology*, *37*, 103-125.
- Coleman, K., & Wilson, D. S. (1998). Shyness and boldness in pumpkinseed sunfish: Individual differences are context-specific. *Animal Behaviour*, *56*, 927-936.
- Dacier, A., Maia, R., Agostinho, D. P., & Barros, M. (2006). Rapid habituation of scan behaviour in captive marmosets following brief predator encounters. *Behavioural Processes*, *71*, 66-69.
- Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, *7*, 734-739.
- Darwin, C. (1872). *The expressions of the emotions in man and animals*. London: Murray.
- Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2003). Realised heritability of personalities in the great tit (*Parus major*). *Proceedings of the Royal Society of London B*, *270*, 45-51.
- Elgar, M. A. (1989). Predator avoidance and group size in mammals and birds: A critical review of the empirical evidence. *Biological Reviews*, *64*, 13-33.
- Endler, J. A. (1993). Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society of London B*, *340*, 215-225.
- Epple, G. (1968). Comparative studies on vocalizations in marmoset monkeys (Hapalidae). *Folia Primatologica*, *8*, 1-40.

- Ferrari, S. F., & Lopes Ferrari, M. A. (1990). Predator avoidance behaviour in the buffy-headed marmoset, *Callithrix flaviceps*. *Primates*, *31*, 323-338.
- Fragaszy, D. M., & Mason, W. A. (1978). Response to novelty in *Saimiri* and *Callicebus*: Influence of social context. *Primates*, *19*, 311-331.
- Friant, S. C., Campbell, M. W., & Snowdon, C. T. (2008). Captive-born cotton-top tamarins (*Saguinus oedipus*) respond similarly to vocalizations of predators and sympatric nonpredators. *American Journal of Primatology*, *70*, 707-710.
- Frost, A. J., Winrow-Giffen, A., Ashley, P. J., & Sneddon, L. U. (2007). Plasticity in animal personality traits: Does prior experience alter the degree of boldness? *Proceedings of the Royal Society of London B*, *274*, 333-339.
- George, C. (1960). Behavioral interactions in the pickerel and the mosquitofish (Doctoral dissertation). Harvard University, Cambridge, Massachusetts.
- Gil-da-Costa, R., Palleroni, A., Hauser, M. D., Touchton, J., & Kelley, J. P. (2003). Rapid acquisition of an alarm response by a neotropical primate to a newly introduced avian predator. *Proceedings of the Royal Society of London B*, *270*, 605-610.
- Godin, J-G. J., & Crossman, S. L. (1994). Hunger-dependent predator inspection and foraging behaviors in the threespine stickleback (*Gasterosteus aculeatus*) under predation risk. *Behavioral Ecology and Sociobiology*, *34*, 359-366.
- Godin, J-G. J., & Davis, S. A. (1995). Who dares, benefits – predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. *Proceedings of the Royal Society of London B*, *259*, 193-200.
- Godin, J-G. J., & Dugatkin, L. A. (1996). Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proceedings of the National Academy of Science of the United States of America*, *93*, 10262-10267.
- Griffin, A. S., Evans, C. S., & Blumstein D. T. (2001). Learning specificity in acquired predator recognition. *Animal Behaviour*, *62*, 577-589.
- Guilford, T., & Dawkins, M. S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behaviour*, *42*, 1-14.
- Gursky, S. (2005). Predator mobbing in *Tarsius spectrum*. *International Journal of Primatology*, *26*, 207-221.
- Hardie, S. M., & Buchanan-Smith, H. M. (1997). Vigilance in single- and mixed-species groups of tamarins (*Saguinus labiatus* and *Saguinus fuscicollis*). *International Journal of Ecology*, *18*, 217-234.
- Hartman, E. J., & Abrahams, M. V. (2000). Sensory compensation and the detection of predators: the interaction between chemical and visual information. *Proceedings of the Royal Society of London B*, *267*, 571-575.
- Hayes, S. L., & Snowdon, C. T. (1990). Predator recognition in cotton-top tamarins (*Saguinus oedipus*). *American Journal of Primatology*, *20*, 283-291.
- Hebets, E. A., & Papaj, D. R. (2005). Complex signal function: Developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, *57*, 197-214.
- Hedrick, A. V. (2000). Crickets with extravagant mating songs compensate for predation risk with extra caution. *Proceedings of the Royal Society of London B*, *267*, 671-675.
- Heffner, R. S. (2004). Primate hearing from a mammalian perspective. *The Anatomical Record Part A*, *281A*, 1111-1122.
- Helfman, G. S. (1989). Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behavioral Ecology and Sociobiology*, *24*, 47-58.
- Heymann, E. W. (1990). Reactions of wild tamarins *Saguinus mystax* and *Saguinus fuscicollis*, to avian predators. *International Journal of Primatology*, *11*, 327-337.

- Hirsch, B. T. (2002). Social monitoring and vigilance behaviour in brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology*, 52, 458-464.
- Iguchi, K., Matsubara, N., & Hakoyama, H. (2001). Behavioural individuality assessed from two strains of cloned fish. *Animal Behaviour*, 61, 351-356.
- Isbell, L. A. (2006). Snakes as agents of evolutionary change in primate brains. *Journal of Human Evolution*, 51, 1-35.
- Isbell, L. A. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evolutionary Anthropology*, 3, 61-71.
- Itoh, K. (2002). Personality research with non-human primates: Theoretical formulation and methods. *Primates*, 43, 249-261.
- Kaplan, G., & Rogers, L. J. (2006). Head-cocking as a form of exploration in the common marmoset and its development. *Developmental Psychobiology*, 48, 551-560.
- Kaplan, G., & Rogers, L. J. (1999). Parental care in marmosets (*Callithrix jacchus jacchus*): Development and effect of anogenital licking on exploration. *Journal of Comparative Psychology*, 113, 269-276.
- Khayutin, S. N. (1985). Sensory factors in the behavioural ontogeny of altricial birds. *Advances in the Study of Behavior*, 15, 105-152.
- Laska, M., Seibt, A., & Weber, A. (2000). 'Microsmatic' primates revisited: Olfactory sensitivity in the squirrel monkey. *Chemical Senses*, 25, 47-53.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68, 619-640.
- Lima, S. L., & Zollner, P. A. (1996). Anti-predatory vigilance and the limits to collective detection: Visual and spatial separation between foragers. *Behavioral Ecology and Sociobiology*, 38, 355-363.
- Macedonia, J. M., & Yount, P. L. (1991). Auditory assessment of avian predator threat in semi-captive ringtailed lemurs (*Lemur catta*). *Primates*, 32, 169-182.
- Magurran, A. E. (1986). Predator inspection behavior in minnow shoals – differences between populations and individuals. *Behavioral Ecology and Sociobiology*, 19, 439-448.
- Magurran, A. E., & Girling, S. L. (1986). Predator recognition and response habituation in shoaling minnows. *Animal Behaviour*, 34, 510-518.
- Martin, R. D. (1990). *Primate origins and evolution*. Princeton: Princeton University.
- Mathis, A., & Vincent, F. (2000). Differential use of visual and chemical cues in predator recognition and threat-sensitive predator-avoidance responses by larval newts (*Notophthalmus viridescens*). *Canadian Journal of Zoology*, 78, 1646-1652.
- Mendoza, S. P., Lyons, D. M., & Saltzman, W. S. (1991). Sociophysiology of squirrel monkeys. *American Journal of Primatology*, 23, 37-54.
- Meredith, M. A., & Stein, B. E. (1983). Interactions among converging sensory inputs in the superior colliculus. *Science*, 221, 389-391.
- Møller, A. P., & Pomiankowski, A. (1993). Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology*, 32, 167-176.
- Murphy, K. E., & Pitcher, T. J. (1991). Individual behavioral strategies associated with predator inspection in minnow shoals. *Ethology*, 88, 307-319.
- Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009). Anti-predator strategies of free-ranging Campbell's monkeys. *Behaviour*, 146, 1687-1708.
- Owings, D. H., & Morton, E. S. (1998). *Animal vocal communication: A new approach*. Cambridge, UK: Cambridge University Press.
- Partan, S. R., & Marler, P. (2005). Issues in the classification of multimodal communication signals. *The American Naturalist*, 166, 231-245.

- Partan, S. R., & Marler, P. (1999). Communication goes multimodal. *Science*, 283, 1272-1273.
- Passamani, M. (1995). Field observation of a group of Geoffroy's marmosets mobbing a margay cat. *Folia Primatologica*, 64, 163-166.
- Peres, C. A. (1993). Anti-predation benefits in a mixed-species group of Amazonian tamarins. *Folia Primatologica*, 61, 61-76.
- Peters, G., & Tonkin-Leyhausen, B. A. (1999). Evolution of acoustic communication signals of mammals: Friendly close-range vocalizations in Felidae (Carnivora). *Journal of Mammalian Evolution*, 6, 129-159.
- Pines, M. K., Kaplan, G., & Rogers, L. J. (2005). Use of horizontal and vertical climbing structures by captive common marmosets (*Callithrix jacchus*). *Applied Animal Behaviour Science*, 91, 311-319.
- Pitcher, T. J., Green, D. A., & Magurran, A. E. (1986). Dicing with death: Predator inspection behaviour in minnow shoals. *Journal of Fish Biology*, 28, 439-448.
- Rowe, C., & Guilford, T. (1999). The evolution of multimodal warning displays. *Evolutionary Ecology*, 6, 655-671.
- Rylands, A. B. (1981). Preliminary field observation on the marmoset, *Callithrix humeralifer intermedius* (Hershkovitz, 1977) at Dardanelos, Rio Aripuanã, Mato Grosso. *Primates*, 22, 46-59.
- Rylands, A. B., & de Faria, D. S. (1993). Habitats, feeding ecology, and home range size in the genus *Callithrix*. In A. B. Rylands (Ed.), *Marmosets and tamarins: Systematic, behaviour and ecology* (pp. 262-272). Oxford, UK: Oxford University Press.
- Schuett, W., & Dall, S. R. X. (2009). Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, 77, 1041-1050.
- Searcy, Y. M., & Caine, N. G. (2003). Hawk calls elicit alarm and defensive reactions in captive Geoffroy's marmosets (*Callithrix geoffroyi*). *Folia Primatologica*, 74, 115-125.
- Seiden, H. R. (1957). Auditory acuity of the marmoset monkey (*Hapale jacchus*). PhD thesis, Princeton University.
- Seyfarth, R. M., & Cheney, D. L. (1980). The ontogeny of vervet monkey alarm calling behaviour: A preliminary report. *Ethology*, 54, 37-56.
- Sih, A., Bell, A. M., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology and Evolution*, 19, 372-378.
- Skals, N., Anderson, P., Kannevorff, M., Löfstedt, C., & Surlykke, A. (2005). Her odours make him deaf: Crossmodal modulation of olfaction and hearing in a male moth. *Journal of Experimental Biology*, 208, 595-601.
- Smith, L. B. (1994). Foreword. In D. J. Lewkowicz, & R. Lickliter (Eds.), *The development of intersensory perception* (pp. ix). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Smith, N. G. (1969). Provoked release of mobbing – a hunting technique of Micrastur falcons. *Ibis*, 111, 241-243.
- Stanford, C. B. (1998). Predation and male bonds in primate societies. *Behaviour*, 135, 513-533.
- Stein, B. E., Huneycutt, W. S., & Meredith, M. A. (1988). Neurons and behaviour: The same rules of multisensory integration apply. *Brain Research*, 448, 355-358.
- Stein, B. E., & Meredith, M. A. (1993). *The merging of the senses*. Cambridge, MA: MIT Press.
- Stewart, L. (2009). *Food calls of the common marmoset*. Honours thesis, University of New England.
- Tinbergen, N. (1959). Comparative study of the behaviour of gulls (Laridae). *Behaviour*, 15, 1-70.

- Troilo, D., Howland, H. C., & Judge, S. J. (1993). Visual optics and retinal cone topography in the common marmoset (*Callithrix jacchus*). *Vision Research*, 33, 1301-1310.
- Uster, D., & Zuberbühler, K. (2001). The functional significance of Diana monkey 'clear' calls. *Behaviour*, 138, 741-756.
- van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour*, 87, 120-144.
- Weinstein, T. A. R., & Capitanio, J. P. (2008). Individual differences in infant temperament predict social relationships of yearling rhesus monkeys, *Macaca mulatta*. *Animal Behaviour*, 76, 455-465.
- Wilson, D. S. (1998). Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London B*, 353, 199-205.
- Yamamoto, M. E., Domeniconi, C., & Box, H. (2004). Sex differences in common marmosets (*Callithrix jacchus*) in response to an unfamiliar food task. *Primates*, 45, 249-254.
- Yorzinski, J. L., & Ziegler, T. (2007). Do naïve primates recognize the vocalizations of felid predators? *Ethology*, 113, 1219-1227.
- Zuberbühler, K. (2001). Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli*. *Behavioral Ecology and Sociobiology*, 50, 414-422.
- Zuberbühler, K. (2000). Causal knowledge of predators' behaviour in Diana monkeys. *Animal Behaviour*, 59, 209-220.