different colour backgrounds, as both females and males were found more often on brown backgrounds (76 and 71% of the time, respectively).

These findings corroborate the Schoener (1975) hypothesis that the green body coloration provides crypsis. The sex difference in coloration, however, also indicates that body colour can be used in sexual recognition. Neither system is perfect, perhaps reflecting conflicting selection pressures on optical signalling.

Alternatively, the determinants of body colour may be more complex than this model predicts. For example, in other species with physiological colour change, body colour indicates both sex and dominant status (Inoué & Inoué 1977). In *A. carolinensis*, male dominance depends on size, with larger and heavier males obtaining more matings (Ruby 1984). If body colour is an indication of dominance, large males may be green and small males may be brown. To test this hypothesis, I compared the SVL of brown and green animals within each sex. Green males were significantly larger than brown males ($t = -3 \cdot 68$, $df = 46$, $P < 0 \cdot 001$), with no difference in size between green and brown females ($t = -0 \cdot 42$, $df = 72$, NS). This finding suggests that for males, body colour may signal both sex and social status. Experimental tests are needed to confirm this hypothesis.

MANDY B. MEDVIN

Psychology Department,
Duke University,
Durham, North Carolina 27706, U.S.A.

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Primate Males Go Where the Females Are

Based on the premise that length of breeding season will be the major determinant of the number of simultaneously fertile females in a group, and that this number will then determine whether a single male can monopolize the mating of all these females, Ridley (1986) predicted an association between reproductive seasonality and the number of males in primate social groups. Because Ridley's test results appear overwhelmingly to support the predicted relationship, one might consider the issue closed beyond the need to explain the seasonality itself. Questions about the methodology, and the presence of a more biologically compelling alternative formulation, suggest otherwise, however.

Ridley's analysis used two dichotomous classifications of primate species, uni-male groups versus multi-male groups, and short versus long birth seasons. All 12 uni-male species were found to have long seasons by this criterion and 18 of 22 multi-male species were counted as having short seasons ($P < 0 \cdot 0000033$). However, a number of methodological problems (plus use of a one-tailed test) inadvertently biased the result in favour of the stated hypothesis. At least six multi-male species in three genera were listed as questionable or not meeting the author's criterion for short birth season but were then included with the short-season species in the test, and the author indicates that a number (unstated) of species with two-male groups were classified as uni-male; reclassifications would in each case go against the hypothesis. Some additional unstated number of species were

excluded from analysis because they included both types of group structures; the effect of their exclusion is unknown. Final probability values will depend on decisions regarding the fate of each problem species; at the very least, the statistical results will be several orders of magnitude weaker, the utility of the classifications are in question, and further examination of the topic is warranted.

Although the classification decisions removed most species that did not conform to the hypothesis, several instances of multi-male groups having long birth seasons remained. Ridley suggested that these birth seasons may be shorter than indicated because reported data were sometimes pooled across groups rather than being reported separately for each group. This point is only partially valid: because males change groups in most male-dispersing species, particularly during the mating season, each group should not be treated as a unit but rather the pooling should be across groups within each local population. Moreover, baboons cannot be counted as having a short season as Ridley suggests it might; the slight degree of seasonality in this genus is of the order of magnitude found in humans. A final methodological concern with respect to seasonality is the biological relevance of the uniform 2-month birth season used by Ridley across all species. For callitricid monkeys weighing several hundred grams, a birth season of 2 months results from conceptions that occurred from four ovulation periods (because endpoints of the birth season each represent ovulation times) but only three ovulations for animals of macaque size or larger.

A male's ability to monopolize conceptions will be a function of the number of females simultaneously in oestrus (e.g. Altmann 1962) and likely to conceive. This number is limited by the number of females in the group; small groups can never have large numbers of females in oestrus, no matter how great the synchrony. Because of nutritional demands for reproduction, females of primates and other species may be more constrained than are males by availability of food resources, and these resources may determine female grouping patterns (e.g. Wrangham 1980; Andelman 1986 for primates). Within any female group size, the number of fertile females simultaneously in oestrus will then result both from birth seasonality and from socially induced oestrous synchrony (e.g. review in McClintock 1983).

A more reasonable alternative single-variable model may result, therefore, from a consideration of female group sizes, rather than birth seasonality, and we can examine the available data (summarized in Andelman 1986; Smuts et al. 1987) from that perspective. Groups of five females or fewer

virtually always have only a single male. When female group size is between five and 10, both uni-male and multi-male groups occur, and reproductive synchrony may be an important factor affecting variability in number of males per group at these intermediate female numbers. Groups with more than 10 females include more than one male. Moreover, demographic stochasticity produces some small groups, even within populations such as those of baboons and the larger-grouping macaques (e.g. Cohen 1972); these small groups, which contain few females, usually include only a single male.

Finally, is it the case, as Ridley argues, that males living in uni-male groups have higher reproductive success than those in multi-male groups because adult sex ratios are usually lower (fewer males per female) in uni-male than multi-male groups? Not necessarily. In such situations a number of males usually live outside mixed-sex groups; male replacement is therefore relatively frequent and often results in infanticide. Consequently, long-term rather than short-term advantage to a male of maintaining a uni-male group versus tolerating the presence of other males will vary and depend partially on the population's overall adult sex ratio. For females, the picture may be clearer. Females are probably at a disadvantage in a uni-male group because of increased risk of infanticide and because female–female reproductive competition will be greater at low sex ratios. Reproductive synchrony may enable females to increase the likelihood of the simultaneous presence of more males in their group. Evidence of flexibility in both birth seasonality and socially induced synchrony among primate females suggest that changing conditions have been a pervasive aspect of the evolutionary context for their reproductive physiology, social behaviour and grouping patterns. As Ridley noted, within-species variability should provide important data for future tests of hypotheses.

JEANNE ALTMANN

Department of Ecology & Evolution,
University of Chicago
940 East 57th Street,
Chicago, IL 60637, U.S.A.
and

Department of Conservation Biology,
Chicago Zoological Society,
Brookfield, IL 60513, U.S.A.

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Unrecognized Anti-predator Behaviour Can Bias Observational Data

Not surprisingly, many animals react to the presence of a human observer with anti-predator behaviour such as mobbing and alarm calling. This fact presents a methodological double-edged sword. It is convenient for an observer to act as both experimenter and stimulus at the same time, allowing him or her to study the effects of posture (e.g. Kruuk 1964), familiarity (e.g. Knight 1984), etc. on the defensive behaviour of the species in question. At the same time, mock predators may bias anti-predator data by, for instance, posing repeated threats that never result in injury. The prey's responses might in turn become inordinately bold, thereby skewing conclusions about predator harassment (Buitron 1983; Knight & Temple 1986). But there is an equally serious bias that can present itself whenever subtle and perhaps unrecognized forms of defensive actions persist in response to an observer who is investigating non-anti-predator behaviour in an otherwise habituated group of animals. The study illustrates one way in which this might happen.

Tamarins are species of the New World primate family, Callitrichidae. Small and sympatric with a variety of aerial and terrestrial predators, tamarins are probably exposed to relatively heavy predation pressures (cf. Goldizen 1987). Among the behaviours that have evolved to meet these pressures are mobbing (Bartecki & Heymann 1987) and high rates of vigilance (Caine 1984). Tamarins demonstrate other, less obviously defensive traits that probably have antipredator benefits as well. Among these are the habits surrounding retirement to the roost each evening. A tamarin group's movement to the roost site (a tree hole, tangle of vines, or, in captivity, a nestbox) has been described as cryptic and concerted (Dawson 1979), and individuals make very little noise at this time (Caine 1987). In addition, Dawson (1979) claims that free-ranging Panamanian tamarins, *Saguinus oedipus geoffroyi*, seem reluctant to enter their roost while being watched. This sort of observation suggests that the secrecy of the nest site is important to the tamarins, but there are no direct tests of that assumption.

I designed a study with captive red-bellied tamarins, *S. labiatus*, that quantified their willingness to enter the nestbox while being observed. In so doing, I also demonstrated that animals may continue to respond to observers with subtle anti-predator behaviour long after 'habituation' has occurred.

Subjects were two groups of red-bellied tamarins living in large indoor enclosures. Group 1 was a family of five; group 2 was a mated pair. The enclosures were fitted with ropes, perches, branches and a nestbox. There was no visual or olfactory contact between the groups, which were housed in different rooms.

Forty-five minutes prior to the usual time of retirement (about 1400 hours), I initiated one of three conditions: (1) observer present and facing the tamarins (I sat quietly in the room, watching the animals); (2) observer present but not facing the tamarins (again I sat quietly in the room but my back was to the monkeys and a video camera recorded the tamarins' behaviour); (3) camera only (in this case a video camera filmed the tamarins but no observer was present). I recorded the exact time when all members of the group had entered the box. Group 1 was observed on 10 days for each of the three conditions. Group 2 was observed for 7 days in each of the three conditions. The order of the three conditions was randomly selected, with the stipulation that all three conditions were represented once during each week of data collection. The study lasted for 5 months.
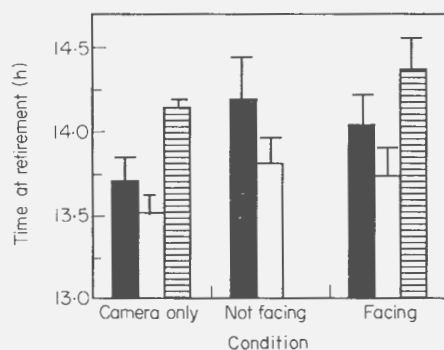
When being watched, the tamarins entered their nestbox about 14 min later than they did with no observer in the room; the delay was by about 18 min in observer-not-facing condition (Fig. 1). The two observer-present conditions did not differ

significantly from one another. The same was true for the second group: the average time of entry to the nestbox was about 19 min later in the observer-facing condition and 29 min later in the observer-not-facing condition. Entry times did not diminish over trials.

Would the same effect appear if the observer was unfamiliar to the tamarins? I repeated the study using six undergraduate students who had no prior exposure to the tamarins. Six trials each of the observer-facing and camera-only conditions were carried out. The tamarins entered the nestbox significantly later (about 14 min) when being watched than they did when not being watched (Fig. 1).

These data lend support to the notion that tamarins, by virtue of their susceptibility to predators, must make careful choices about when and perhaps where to roost each night. Entering a nest site while being watched by a potential predator would undoubtedly be a risky thing to do. Indeed, my results suggest that it is not merely being watched that is disconcerting; when I sat in the room with my back to the tamarins, they delayed their entry into the box as much as when I was facing them.

The results of this study can be taken even more seriously when one considers that I, as a very familiar stimulus, elicited the same response as did the unfamiliar observers. This leads one to consider the potentially troubling methodological implication of the current study: a 'habituated' group of animals may continue to respond defensively in ways that are unrecognizable by the investigator. For example, behaviour that makes animals vul-

nerable to predatory attacks (e.g. grooming or copulation) may be reduced in frequency, form, or duration when an observer is present. Such alterations in the patterns of certain behaviour may bias the results of a study in important ways. In the case of the sleeping habits of tamarins, an investigator whose interest and expertise are not in anti-predator tactics, but in circadian rhythms, might overestimate the length of the tamarins' day based on his or her observations of retirement times. If the investigator used a blind or collected his or her data by video camera, the results could be different (cf. Candland et al. 1972).

Many of us have no choice but to observe our animals without the use of a blind. Hopefully, we will be justified in assuming minimal effects as a function of our presence. Certainly, however, the remarks that many investigators make about habituation should be made with circumspection. Predation-related concerns may alter the behaviour of some species for the life of the study.

NANCY G. CAINE

Department of Psychology,
Bucknell University,
Lewisburg, PA 17837, U.S.A.

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Figure 1. The average time ($\pm$SE) that the tamarins entered the nestbox. □: group 1 in the presence of the familiar observer; ■: group 2 in the presence of the familiar observer; ▤: group 1 in the presence of the unfamiliar observers. The camera-only conditions differed significantly ($P < 0.05$) from the observer-present conditions.