result in suffering. The list of small probably differing little activities found in current systems. Not surprisingly the insufficient to allow animals. Furthermore, as the is a relative measure, the environmental deprivation that is almost indeterminate. The regulatory systems on the grounds of requirements defined by the would appear to leave only a tiny of safety between well

cans could be designed to standards by catering for the and other luxury activities. For such designs would not be of ethological needs, but the to, that luxury activities at great deal of certainty when suffering absent or at a much would also serve to and often poorly described our domestic animals. By catering for some mix-

ives of our farm animals, treat them rather as we do

ALESTAIR LAWRENCE

of Agriculture.

U.K.

n. J. 1973. The role of play in reparative observations of spir- Primates, 14, 369-381.

m. J. 1976. Benefits of food from a laboratory simulation. Z.

log structure and functions of beeh (Ovis canadensis). J. Zool.,

Easter here name their pecu-

lity and the measurement of live. Behav., 31, 1195-1205.

Play, Behaviour. New York: w.


reparative method in studying


Received 7 May 1988, revised 9 June 1988; MS. number: 3084

Consumer Demand Theory and the Assessment of Animal Welfare: A Reply to Lawrence

Lawrence’s (1987) comments on my (1983) paper are misleading in two respects. First, he concludes that the results show that dustbathing in the hen is not under regulatory control. I was careful not to draw this conclusion since I did not feel it is justifiable by the evidence. Hens perform many other behaviours in litter besides just dustbathing (a relatively rare behaviour) so that ‘access to litter’ should not be equated with ‘dustbathing’. It is quite possible that dustbathing is under regulatory control, even that it shows ‘resilience’ and that the apparent lack of resilience for access to litter was due to the hen’s willingness to forego other litter-related activities. In any case, I did not make the connection between ‘regulated’ behaviour and ‘necessity’. That is Lawrence’s, in my view, incorrect interpretation. Criticism of the above should surely be confined to the author’s own conclusions, not the critic’s mistaken interpretations!

Secondly and more seriously, he implies that I argued that once behavioural ‘necessities’ had been catered for, we need worry no more about the animals’ welfare. I did no such thing. My point was that if we wish to improve the welfare of animals our first priority should be to remove the major sources of suffering. The realities of commercial farming mean that we cannot ‘at a stroke’ improve the living conditions of farm animals in every way we might want to. We may be able to make some improvements; however, it is important that we concentrate our efforts in those areas that make the most difference to the animals’ welfare. I put forward a framework for deciding what changes might be most important to the animals themselves.

Lawrence urges us to treat farm animals as we do ourselves. Perhaps he could use this bevel to accept the point of what I was saying if he were suffering from a variety of ills and not all of them could be removed at once, would he not feel that top priority should be given to the removal of what he regarded as the major sources of his suffering first?

MARIAN STAMP DAWKINS


References


Received 30 July 1986; MS. number: 329

Indirect Costs of Play: Cheetah Cubs Reduce Maternal Hunting Success

Because the functions of play are still unknown, and are proving particularly difficult to investigate (Caro & Atewi 1985; Marin & Caro 1983), it is becoming increasingly important to marshal evidence concerning the costs of play so as to gain a minimum estimate of the magnitude of its proposed benefits. Data on the time and energy costs of play have been generated from laboratory studies of domestic cats (Martin 1984), while its survivorship costs are limited to a small number of anecdotal examples from the field (Fagen 1984). Both the apparently low time and energy costs of play, and the paucity of accounts of playing animals suffering injury, suggest that play may only have marginal benefits to be favoured by natural selection, but other, indirect costs may yet to be considered. Here I present data to show that the costs of play can not only affect young animals directly, but can affect them indirectly through their effect on parents on whom they depend.

Data on the outcome of 653 hunts by 36 different cheetah, Acinonyx jubatus, mothers with dependent cubs, aged between 1-5 and 18 months, were collected in the Serengeti National Park, Tanzania during 54 watches, each lasting 1-7 days, of cheetah families (3773 hours in total; see Caro & Collins 1987). A hunt was defined as beginning when a mother cheetah started to stalk, trip towards, crouch at, rush, or cluse a group of prey animals; hunts that involved large eubs only and not their mothers were excluded from analysis.

Short Communications
Observers can immediately recognize when prey have been a cheetah by their alert posture and variety of anti-predator responses (Cari 1986). A hunt ended when mothers stopped their advance towards prey after prey had been seen, when they walked away from prey they had been hunting, or failed to catch their quarry at the end of the single chase that characterized cheetah hunts (see Wroe, 1975; Amann & Amann, 1984). Although hunts varied in duration from 1 to 165 min, they were normally separated by hours or even days and were thus treated as independent.

Seventy-three per cent (478) of these hunts failed and the reasons for failure were recorded as follows. (1) Cub play: prey becomes aware of the cheetah’s presence because of a cub’s actions prior to their mother’s final rush towards the prey, for example by sitting up or moving when the prey was looking in their direction. (2) Cub play: prey alerted by cubs playing with each other, or by cubs chasing other species such as zebra, Equus burchelli, which are far too big to be captured by small cubs. Play was defined as locomotor activity in which motor patterns resembling those used in serious functional contexts were used in an exaggerated, repetitious, or fragmented form, and which appeared to have no immediate benefits (see Martin & Cari, 1985 for full definition). (3) Mother seen: prey alerted to cheetahs’ presence because of the mother’s actions before she started her rush. (4) Mother or cub seen: in some hunts it was difficult to be absolutely sure whether the mother or a cub was responsible for prey noticing the cheetahs, and this was recorded separately. (5) Starts rush too early: mother starts her uncoordinated sprint towards the prey well outside the distance it can be easily captured (in practice 30 m, Cari 1986). (6) Outrun by prey: rush starts within this distance but the prey gains distance or outmanoeuvres the mother during the chase. (7) Prey leaves the area: the prey moves away from the cheetahs without being aware of their presence, further advance is fruitless because the distance to the prey is increasing, or the prey has moved into open vegetation where further uncoordinated approach is impossible. (8) Hunt not serious: the hunt appears to the observer to be opportunistic for a variety of reasons, e.g. the prey is larger than that normally captured, or the mother is already satiated. (9) Other reasons: all other possibilities, e.g. the appearance of a lion, Panthera leo, or spotted hyena, Crocuta crocuta, which inhibits cheetahs from hunting; when a newborn gazelle hid in long grass and could not be located; or when reasons for failure were unclear.

Table 1 shows that cub activity caused 78 (16.3%) hunts to fail. This increased to 102 (21.3%) when hunts where it was unclear whether the mother or cubs had been seen were included. Interestingly, few hunts failed because prey outran or outmanoeuvred mothers once a chase had begun. Separate analyses, not presented here, revealed there were no effects of cub age on any of the reasons for failure. Cub play per se accounted for seven of the 78 (9.0%) failures definitely caused by cubs, and 1.5% of all the mothers’ hunts that failed. This represented a mean of 6.6% of the time spent in unsuccessful hunts by those mothers who were afflicted by their cubs’ play or 4.6% of the total time they spent hunting. Furthermore, the average weight of prey lost in the hunts disrupted by cubs’ play was 17.6 kg, about the weight of an adult female Thomson’s gazelle, Gazella thomsoni (see Blumenstock & Cari, in press). This represented an average of 46.6% of the weight of prey these afflicted mothers actually managed to capture during the time their litters were observed. Nevertheless, it must be noted that even if these hunting episodes had not been disrupted by cub play, they could have subsequently failed for some of the reasons given in Table 1.

These data suggest that cheetah cub play, and indeed other aspects of cub behaviour, has more than incidental impact on the hunting success of their mothers. By reducing the amount of food that mothers can capture for them per unit time, play will lower cub energy intakes, and will also cause them to experience somewhat longer intervals between solid feeds. Decreased hunting success due to play may even reduce the quantity of milk mothers can provide, affecting 6-14-week-old cubs who have left the den but are still nursing (Schaller, 1972). Moreover, cubs will suffer energy and time costs by being forced to accompany their mothers greater distances in search of new prey.
addition to the time and energy expended in their own playful activities. As play will similarly reduce mothers' own energy intake and cost her extra time in hunting, postulated benefits that cubs may accrue through play will, in part, have to outweigh costs to the mother, as well as costs to the players. Future studies of play in carnivores therefore need to consider its indirect costs to offspring and hidden costs to parents when assessing overall costs of play.

I thank the Government of Tanzania for permission to conduct research, the Royal Society for funding, and Steve Albon, Monique Bergerhoff-Mulder, Montse Comendido and Paul Martin for comments.

T. M. CARO

Sub-department of Animal Behaviour, University of Cambridge, Madingley, Cambridge CB3 8AA, UK, and Serengeti Wildlife Research Institute, P.O. Box 661, Arusha, Tanzania.

References


Received 2 June 1986; revised 8 July 1986. MS. number: 314

Variation in Hoarding Behaviour in Southeastern P. leucopus

Hoarding, the movement of potential food items from one location to another before consuming them at a later time (Smith & Reichmann 1984), is a preparatory adjustment compensating for conditions of high metabolic demand coupled to a low supply of energy. Roberts (1979) suggested that hoarding evolved under the selective pressures imposed by seasonal fluctuations in food availability. If hoarding is an adaptive response to stressful environments, then it should be more pronounced in species inhabiting cold environments or those in which food becomes seasonally scarce. Although Barry (1976) demonstrated that northern P. parvus (deermice) are more prone towards hoarding than southern forms of deermice, relatively few studies have compared hoarding in different P. parvus species. We assessed laboratory hoarding tendencies in two species with different elevational distributions, predicting that the more montane form would display higher hoarding tendencies and cache more food than its lowland congeners.

Captive-born offspring of wild P. maniculatus nubiferus (trapped in Macon County, North Carolina, at 1000 m) and P. leucopus leucopus (trapped near Clemson, South Carolina, at 250 m) were maintained until weaning in a breeding colony (20-23 C, 12L:12D). They were acclimated for 5 months at a temperature of 5 C and on a photoperiod of 9L:15D before hoarding tendency was assessed (under these conditions) in individual home cages with attached runways allowing 24 h access to food hoppers. Hoppers were provisioned with 25 pre-weighted food pellets (identical to those eaten previously) that had been sorted to a uniform size of 3.5-4.0 g.

Once daily, we counted and weighed the pellets remaining in the food hopper and those that had been transported into the home cage. All food was then removed from the home cage, and the hopper replenished with fresh pellets. Three measures; hoarding score (Morgan 1945), hoarding mass and food consumption, were recorded for each mouse on each of 5-9 consecutive days. The proportion of hoarders within each species was compared using the G-statistic. Mean daily hoarding score, hoarding mass and food consumption were calculated for each individual, and data were subjected to two-way ANOVA and Student's t-test.

P. leucopus displayed a greater tendency (P < 0.05) to hoard than did P. maniculatus (Table 1). Of the P. leucopus, 83% engaged in hoarding, whereas only 31% of P. maniculatus hoarded. P. leucopus also displayed significantly (P < 0.01)