African wild dogs test the 'survival of the fittest' paradigm

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Recd 05.02.03; Accptd 24.02.03; Online 02.04.03

Charles Darwin first used the term 'survival of the fittest' in the 5th edition of *The origin of species*. A literal interpretation implies that predators will selectively prey upon the weakest members of a population. We demonstrate that this is true for African wild dogs hunting impala.

Keywords: predation; survival; Darwin

1. INTRODUCTION

The phrase 'survival of the fittest' first saw the light of day in March 1852 in an essay by Herbert Spencer, in the journal *Leader* (Spencer 1852). However, it is Charles Darwin's classic usage in the 5th edition of *The origin of species* (Darwin 1869) that is now best remembered.

This preservation of favourable individual differences and variations, and the destruction of those which are injurious, I have called Natural Selection, or the Survival of the Fittest.

A literal interpretation of the survival of the fittest is the idea that predators will feed selectively on the weakest individuals within a population.

African wild dogs, *Lycaon pictus*, constantly live on an energetic knife-edge due to the very high energy costs incurred by their method of hunting (Gorman *et al.* 1998). Their daily energy expenditure of up to 20 MJ is five to six times basal metabolic rate (BMR) and is close to the absolute physiological limit of six to seven times BMR suggested for sustainable metabolic rate (Hammond & Diamond 1997). One might expect, therefore, that dogs would select individual prey that are easiest to catch, and that incur the least energy expenditure. Here, we show that African wild dogs exploiting impala *Aepycerus melampus* in the Save Valley Conservancy, Zimbabwe do select those individuals that are in poorer condition.

2. MATERIAL AND METHODS

At times of food shortage, ungulates metabolize stored body fat, with the fat in the marrow of the limb bones being used last (Brooks *et al.* 1977). Consequently, low bone marrow fat levels indicate individuals that are in very poor condition (Bear 1971). We collected marrow from the femurs of 242 adult impala killed by dogs and from a random sample of 67 adults shot, non-selectively, at night. A portion of bone marrow was removed from the central white portion of the femur of the hind leg of the carcass, avoiding the haemopoietic end portions of bones. The samples were oven dried at 60 °C until they reached constant weight.

Figure 1. Fat levels in the femur marrow of adult impala killed by wild dogs (filled circles), or shot (open circles) during the wet (open bar) and dry (hatched bar) seasons.

As an index of fat content we expressed the dry weight of the marrow as a percentage of the fresh weight, minus 7%; the constant representing the non-fat residue, which varies from 5% to 10%, with a mean of 7.1%, in African ungulates (Brooks *et al.* 1977).

3. RESULTS

The marrow fat levels in the animals culled by humans were relatively high and varied little throughout the year, but levels in dog kills were generally lower, particularly so during the wet season (figure 1).

The differences in marrow fat content were analysed by a residual maximum-likelihood algorithm using the Wald test to provide efficient estimates of treatment effects in unbalanced designs (Patterson & Thompson 1971). The interaction between season and whether dogs or humans killed the impala was significant (Wald = 4.18, d.f. = 1, $p = 0.041$). There were no seasonal differences in the bone marrow fat of impala culled by humans (standard error of the difference (s.e.d.) = 4.15) but seasonal differences among dog kills were significant (s.e.d. = 2.62). In the wet season, marrow fat levels were significantly lower in impala killed by dogs than in those culled (kill = 40.39%, cull = 55.56%, s.e.d. = 3.83). A weak trend was present in the dry season, the direction being in agreement with Darwin's prediction (kill = 54.18%, cull = 59.36%, s.e.d. = 3.06).

4. DISCUSSION

This study clearly demonstrates that wild dogs selectively predate those individuals within a population that are in poorer condition. Fit impala do indeed have the better chance of survival.

- Bear, G. D. 1971 Seasonal trends in fat levels of pronghorns, *Antilocapra americana*, in Colorado. *J. Mamm.* **52**, 583–589.
- Brooks, P. M., Hanks, J. & Ludbrook, J. V. 1977 Bone marrow as an index of condition in African ungulates. *S. Afr. J. Wildl. Res.* **7**, 61–66.
- Darwin, C. 1869 *On the origin of species by means of natural selection*, 5th edn. London: John Murray.
- Gorman, M. L., Mills, M. G., Raath, J. P. & Speakman, J. R. 1998 High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature* **391**, 479.
- Hammond, K. A. & Diamond, J. 1997 Maximal sustained energy budgets in humans and animals. *Nature* **386**, 457–462.
- Patterson, H. D. & Thompson, R. 1971 Recovery of inter-block information when block sizes are unequal. *Biometrika* **58**, 545–554.
- Spencer, H. 1852 The development hypothesis. *The Leader* 20 March.