# Socio-ecological models for red fox populations subject to fertility control in Australia

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Immuno-contraception is being developed in Australia to control populations of the introduced red fox (*Vulpes vulpes*). One possible adverse response is compensatory reproduction which is being studied in captive and wild populations. In the Northern Hemisphere, red fox populations subject to marked changes in food supply, as experienced also in Australia, respond numerically and functionally. Ovulation rates and cub production follow suit, but the evidence on mean litter size is equivocal. At high food supplies, groups form with more cubs born to them than to mated pairs. There may be little agonistic behaviour as well, and the role of 'helpers' in groups needs elucidation. The circumstances under which home ranges are defended in whole or in part is uncertain also. No general hypothesis on territoriality in the red fox seems achievable at present, but some ideas from recent specific and general hypotheses are testable. It is suggested that the concept of 'fugitive species' should be examined for an understanding of flexibility in the socio-ecological system of the red fox.

## 1. Introduction

Olina (1622) wrote of the nightingale that "it sings in its freehold". That emphasis upon landholding, as ascribed to birds then, and by 17th and 18th Century writers to follow, is mentioned in the delightful Introduction by Huxley and Fisher to the 1948 edition of Howard's (1920) seminal study of territory in birds. The concept of home range is more recent. Burt (1943) drew on history also, quoting Seton (1929) as follows: "In the idea of a home region lis the germ of territorial rights". According to Lockie (1966), a territory may be tightly definable, but home range

"is a more loosely organised system". Those dual functions for land, use of all of it but defence of the whole or a part, may alter relatively in space and time. For example, there may be few agonistic interactions or many, and defence (see Jewell 1966) may be of localised resources only (food; dens) or of outer limits of home ranges. Seasons, species, age structures, sex ratios, reproductive status of individuals, density of population, neighbours, resources are all factors, some of which may interact.

In this paper a broad view has been taken of sociality for the red fox (*Vulpes vulpes*) which encompasses demography, reproduction and ter-

ritoriality. Many papers on the red fox concentrate on home-range and territory in that order, with non-overlapping and contiguous home ranges accepted as territories without evidence in some cases. There are fewer studies of sociality which is best understood in captive and urban populations (Harris 1977, 1979, Macdonald 1977, 1979, 1980, Saunders et al. 1993). And there are even fewer papers which link sociality, reproduction and populations dynamics to considerable shifts in food supplies, those of von Shantz (1984), Lindström (1986) and Zabel & Taggart (1989) being exceptions which are utilised here for an understanding of how the red fox may operate in Australia. Complicating matters is that there are three territorial hypotheses for the red fox: (a) the Resource Dispersal Hypothesis, spatially (Macdonald 1983) and temporally (Carr & Macdonald 1986); (b) the Constant Territory Size Hypothesis (von Schantz 1984); and (c) the Territory Inheritance Hypothesis (Lindström 1986). There is, however, sufficient flux in theory and understanding for Stamps (1994) to strongly challenge current assumptions underlying the concept of territoriality in general (see Discussion).

This paper first summarises what is known of the red fox in Australia, and outlines the novel approach of immuno-contraception which is being developed for control of their populations. It then considers the literature for indications of socio-ecological models which may apply for the species in Australia with its varied and episodic environments, because so little is known of the fox's ecology and sociality. Of particular relevance are the effects of food supplies and dominance hierarchies on social dynamics and organisation, on group formation and disassemblage and on reproductive fitness of group members, and in particular what circumstances drive those transformations, intrinsic and extrinsic.

*Immuno-sterility proposed for controlling red fox populations in Australia*

There is an urgent need to control fox populations in the southern half of Australia for the threat to wildlife (Kinnear et al. 1988, Burbidge 1989). Because of the scale of the problem, a novel method of control, immuno-contraception, is

under study for red fox populations and for its main prey, the eruptive European rabbit, *Oryctolagus cuniculus*, (Bradley 1994, Tyndale-Biscoe 1994). Theoretically, immuno-contraception should have the advantage over conventional controls in that normal hormonal systems should continue to function unaffected such that territorial integrity, mating systems, feeding patterns, and other fundamental attributes of sociality should remain in place. Such issues are testable, and experiments with captive and free-ranging foxes have begun in Australia (see below). A particular issue to examine if immuno-contraception is to succeed ecologically is whether fertility and fecundity increase through compensatory reproduction which could arise in the following ways:

a) If too few vixens are sterilised in any population;

b) If fecundity of subordinate vixens increases when dominants are sterilised;

c) If reproduction increases as populations decline and more food is available.

The most difficult case for the control of populations would be high densities, high food supplies, and a high capacity for socio-ecological systems to accommodate imposed infertility. Given the changeable weather patterns in Australia due to El Niño events, there is likely to be considerable interplay between socio-ecological factors and the usual 'feast or famine' in food supplies. Caughley (1987) has pointed out for Australia that "the forces causing temporal variation may be so powerful, continual and multi-directional that the 'equilibrium' is seldom or never occupied" (see also Caughley & Gunn 1993).

## 2. The red fox in Australia

### 2.1. Predator-prey relationships and wildlife conservation

Both red fox and European rabbit were introduced to south-eastern Australia several times in the mid-1800's for hunting (Rolls 1969). The rabbit spread both north and west much faster than the fox, the two species reaching about the
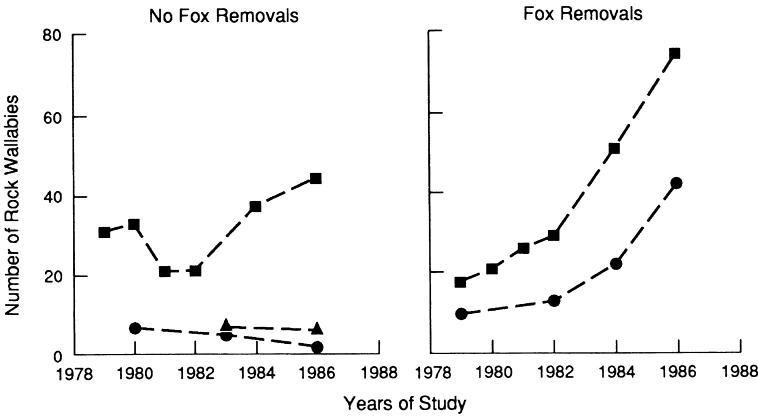
Fig. 1. Sustained increase in populations of rock-wallabies (*Petrogale lateralis*) when red foxes (*Vulpes vulpes)* were controlled in Australia. (Redrawn from Fig. 4, Kinnear et al. 1988).
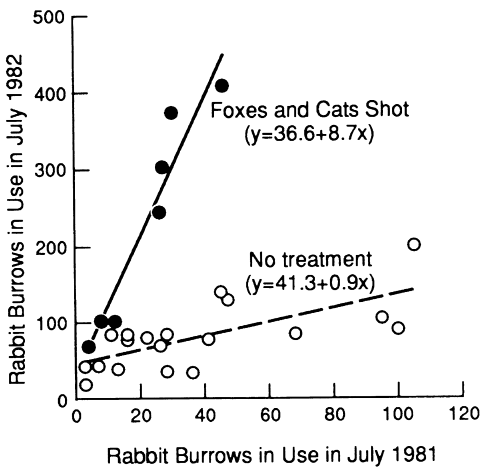


Fig. 2. Increase in populations of wild rabbits (*Oryctolagus cuniculus*) in Australia when red foxes (Vulpes vulpes) were persistently shot compared with relatively steady, low populations otherwise. (Redrawn from Fig. 5a Newsome et al. 1989).
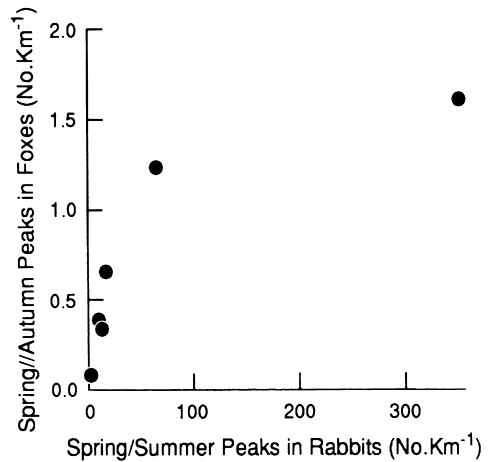


Fig. 3. Numerical response of red foxes (*Vulpes vulpes*) during an eruption of wild rabbits (*Oryctolagus cuniculus*) in Australia. (Adapted from Pech et al. 1992).

same northern limit around 1910 and 1940 respectively (Stoddart & Parer 1988, Jarman 1986). Today, they form a dominant predator-prey system in most ecosystems in semi-arid Australia. The environmental damage caused by the rabbit has been clear from the start (Rolls 1969); but Kinnear et al. (1988) showed clearly that only after fox populations were controlled, were the decline and extinction of rock wallabies (*Petrogale lateralis*) in south-western Australia reversed (Fig. 1). Up to 18 species of marsupial and native rodent within a critical weight range, 35 g–5.5 kg are extinct, and about as many are endangered (Burbidge 1989, Short et al. 1992,

Dickman et al. 1993). Ground-dwelling birds are at risk, e.g. the semi-arid mound builder, the mallee fowl (*Leipoa ocellatus*) (Priddel & Wheeler 1994). Recent evidence from Sweden shows that mountain hare, capercaillie and grouse populations increased after fox populations were reduced during a severe outbreak of mange (*Sarcoptes scabei*) (Lindström 1991, Lindström et al. 1994).

The interaction between foxes and rabbits is doubly significant because low populations of rabbits increased significantly when foxes were experimentally removed (Newsome et al. 1989) (Fig. 2). Foxes responded numerically (Fig. 3)

and functionally when rabbits erupted. After collapsing in drought from 370 to 2–3 km$^{-1}$, however, fox predation regulated the rabbit populations at densities between about 8 to 12 rabbits km$^{-1}$ (spotlight counts) (Pech et al. 1992, Pech et al. space in press). Prey switching to wildlife may be an issue at such times, and with feral cats also, as their diet responds functionally to rabbits (Catling 1988). When Marlow (1992) removed rabbits by destroying warrens with a tractor pulling a deep plough on a 834 ha in semi-arid western New South Wales, scat analyses indicated a decline of rabbit in the diet of foxes from about 30% to about 20%, with ground birds (mostly quail) increasing from 1.8 to 11.9% ($P < 0.001$). Such switching may result from conventional control of rabbit populations, and is an issue to examine in detail if immuno-contraception succeeds.

## 2.2. Demographic evidence on hunting strategies and defence

No group hunting is reported in foxes, and so what is the function of their groups? Foxes may live in spatially condensed groups at high densities, with the extra vixens sometimes breeding and/or 'helping' rear the dominants' cubs (Harris 1977, 1979, Macdonald 1977, 1979, 1980, von Schantz 1984, Mulder 1985, Lindström 1988). How foxes function socially in Australia's varied environment is unknown. Foxes may be seen alone commonly, which may indicate that simple social organisations prevail, but not necessarily. Many foxes may be seen around carcasses, perhaps indicating groups but may be an aggregation response to feed also. Studies of sociality have begun (T. Bubela in prep.), but evidence for social groups is mostly circumstantial at present. For example, on 2.4 km$^2$ of temperate farmland Coman et al.(1991) found 19 breeding pairs with overlapping home ranges averaging 6.1 km$^2$, but 69 foxes were shot in 3 d a few months later when cubs should have been dispersing (Coman 1992), indicating that there may have been groups also. Known home range sizes (Saunders et al. in press), are 9.3 km$^2$ in the alpine zone, 1.6 km$^2$ in

sub-alpine areas, and 3.4 km$^2$ in farmland, with 4.2 km$^2$ in mixed forest and heathland on the eastern coast (Phillips & Catling 1991). These values are intermediate to known extremes worldwide, 0.9 km$^2$ in urban England to 34 km$^2$ in the Arctic (Macdonald 1987).

Although studies are in progress (T. Bubela unpubl., J. McIlroy in prep.), the only social study of wild foxes in Australia is by Birchfield (1980) on hunting strategies, scent-marking and interactions with neighbours in three fox families (pairs and cubs) and two non-aligned males. Although sizes of home ranges were not known, hunting areas (mostly for rabbits), were small, 6 ha for the group most watched and 16–60 ha for a neighbouring pair, and they did not overlap after breeding. Foxes mostly hunted alone but occasionally pairs hunted a large rabbit, or worked in tandem where rabbits were common. Vixens did most of the active scent-marked (urine) around the hunting area especially while rearing young and for three months afterwards, and adult males did the scent-marking when expanding the hunting areas (see Burrows 1968) onto land left vacant after one group was poisoned by a farmer. No dominance/subordinate reactions were seen between dog foxes and vixens, and no signs of proximity intolerance until mid-autumn. Residential neighbours within 50 m of one another did not react, not even when the expanded hunting areas overlapped in autumn, and they ignored chemical signals until active defence of hunting areas began in autumn (see comments from Stamps 1994 below). Both juvenile and adult resident males defended hunting areas, always against transgressing non-resident males which, after a few losses and pursuits, voluntarily retreated if the resident was present. Dog foxes helped provision the vixen with rabbits and birds prior to birth of cubs only. Both sexes played with young cubs but only the vixen did so as they grew, and only she took them hunting until late summer when they hunted alone or sometimes in pairs. The mothers drove them off by early autumn, which contrasts with the Zabel and Taggart's (1989) report that dispersal began when retrieval of food for them became intermittent (see below).

# 3. Evidence for flexibility in social systems of wild foxes from the northern hemisphere

Three studies from the northern hemisphere are examined here for evidence of socio-ecological adaptability in red foxes to changing food supplies.

## 3.1. Sweden (von Schantz 1981a, b, 1984, Lindström 1980, 1982, 1986, 1988, 1989, Lindström et al. 1981).

The relevance of the two sets of Scandinavian studies to Australia lies in the changes to demography, reproduction and social structures in fox populations as food supplies first increased and then decreased. Also, an outbreak of sarcoptic mange (*Sarcoptes scabei*) reduced fox populations drastically, so enabling Lindström (1991) to examine ovulation rates and recruitment for evidence of compensatory responses. Lindström's (1988, 1989) main study site was in boreal forests at Grimsö, south-central Sweden, where vole populations cycle over a 4 yr period with an average biomass of 9.3 kg km$^{-2}$ (Lindström et al. 1981). The study area of von Schantz (1984) was further south in arable regions near Revinge where microtine populations do not cycle and are a minority prey (<6 kg km$^{-2}$) (see Hansson & Henttonen 1988, Hanski et al. 1991, for the significance of that difference in population fluctuations). At Revinge rabbits (*Oryctolagus cuniculus*) were the main prey whose numbers rose over 3 yr to a peak biomass of 700 kg km$^{-2}$ before declining for 5 yr to a low of 200 kg km$^{-2}$ (von Schantz 1984; Lindström et al. 1981).

Lindström (1989) concluded that food supplies were the primary driving force for fox populations. Of most note for the theme of this paper, Lindström (1988) showed that ovulation rates increased with the food supply, and concluded that the trend in mean litter size (see Fig. 4) was also significant. A one-tailed test was applied in that paper, but a two-tailed test has been used here (see Lombardi & Hurlbert 1995)
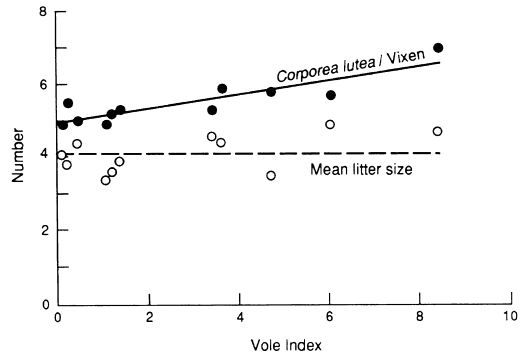


Fig. 4. Increase in ovulation rates (*P* < 0.01) in the red fox (*Vulpes vulpes*) but not of mean litter sizes (*P* > 0.05) in response to fluctuating abundances of voles (*Clethrionomys glareolus, Microtus agrestis*) in Sweden (From Table 1, Lindström 1988). In contrast to the original analysis, probability levels based on two-tailed test were used here (see Lombardi & Hurlbert 1995). The dotted line is through the mean.

which indicates that the slope for the mean litter sizes is not significant as shown in Fig. 4. Von Schantz, (1984) data also showed no significant trend in mean litter size with increase in rabbits, but there was increase in the total number of litters (Fig. 5) and the proportion of sub-adult foxes in the populations also. Those results present the anomaly that, if rates of ovulation, frequencies of whelping and proportion of sub-adults in the population increase with food supplies, why not mean litter size? By counting uterine scars, Englund (1970) found variation in the mean litter size with changing vole abundance; and Lindström (pers. comm.) similarly measured an increase. Uterine resorption may be involved (see Lindström 1991), and Hartley et al. (1994) reported that reproductive losses could be related to lowered progesterone levels (possibly due to inadequate luteotrophic support from prolactin), related to social stress. Though not examined in these papers, compensatory infanticide at or near birth may also be involved as found by Bakken (1991). With the evidence equivocal, one issue to address for the control of populations by immuno-contraception in Australia is regulation of litter size.
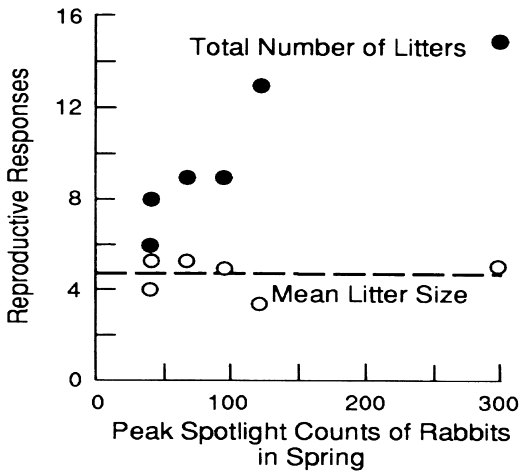
Fig. 5. Numerical responses in cub production in red foxes (*Vulpes vulpes*) but not of mean litter size, to varying populations of rabbits *(Oryctolagus cuniculus)* in Sweden. Probability levels are based on regression analysis. The dotted line is through the mean. (Interpolations from Figs 1 & 2, von Schantz 1984a).

In both study areas, maximum home ranges of breeders were similar, 6.9–6.5 km$^2$ (Lindström et al. 1981), with those at Grimsö overlapping a little but basically being independent, whereas there was considerable overlap at Revinge. About half of the adult population at Revinge were considered to be non-breeders, mostly females. They lived within home ranges of the breeders on small sections (3.6 km$^2$) which became smaller (2.7 km$^2$) after rabbit numbers collapsed The role of non-breeders in groups remains uncertain. Although they visited dens, they did so about ten times less than the one mother which was followed by radio-tracking. Whether visits by non-breeders represent 'helping', i.e., parental care, is not known. The generalities of these issues for non-breeders require confirmation. For example, one classified non-breeder is recorded as adopting the litter of a vixen which died, and cubs of two litters were found on the one home range at the peak in rabbit densities (von Schantz 1984). There was some overlap in ranges however.

All manner of evolutionary advantages may accrue if super-numerary foxes are offspring or related to other breeders in a home range; but such relationships have yet to be demonstrated conclusively to my knowledge. Von Schantz

(1984) has suggested that the Revinge foxes exhibited an early 'primitive' stage in group living, and he accepted Brown's (1978) view that 'helping' may be a consequence of high food supplies rather than its cause. That is as in the example of Zabel & Taggart (1989) below: extra vixens were tolerated when there was no shortage of food. Lindström (1986) outlines the advantages to foxes if they were related on any home range, directly and for the future. Relatedness would support Emlen's (1978) study of birds which suggests that it represents 'insurance' (see Insurance Hypothesis of Brown 1978, and Woolfender & Fitzpatrick 1978). If relatedness is demonstrated, that would leave the issue of whether tolerance would be extended to unrelated dispersing juveniles and vagrants, or indeed to neighbouring resident foxes. These issues require examination also.

## 3.2. Round Is, Alaska (Zabel & Taggart 1989)

The study of the red foxes on that small island (3 km$^2$) indicates that territorial grouping may not be an obligatory corollary of high densities of 9–10 km$^{-2}$. There were 27–30 foxes which belonged to 15 groups, but there was little evidence of territoriality as such, defence being of dens and not of food or other spatial resources which were shared. About 75% of foxes were non-breeders on average, and almost half of those lived on parts of group ranges, with a notable lack of antagonistic behaviour towards them. Supernumerary foxes did not associate with reproductive groups or den-sites.

The usual food supply was a large nesting colony of seabirds (*Uria aalge, Rissa tridactyla*) which almost totally failed to breed in the last half of the study under conditions familiar to Australia, an El Niño event. No deaths through starvation or fighting were recorded among foxes nor expansions of home-ranges, but there was considerable loss of social complexity. Bigamy disappeared, the modal size of groups declined from three to two, there were more non-breeders, and one female became monogamous and a monogamous female became a super-numerary. The number of cubs born was halved, but survivorship to 1 yr remained around 50%. Two mothers
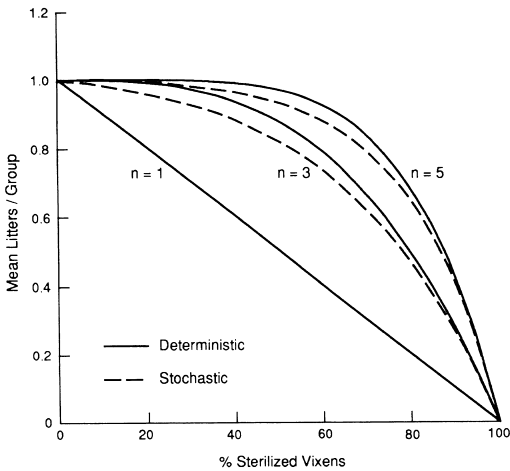
Fig. 6. Models of the reproductive responses in families of red foxes (*Vulpes vulpes*) assuming different numbers of vixens (*n*) and compensatory breeding in subordinates with the dominant vixens sterilised. (Apapted from Caughley et al. 1992).

## 4.1. A theoretical mathematical model (Caughley et al. 1992)

The model assumed a population of fox families each with an adult pair and up to four vixens which were subject to varying levels of immuno-contraception. It was assumed that dominance was linear, and that sterility of the dominant vixen resulted in breeding of subordinate vixens. The response curves generated (Fig. 6) present the proportion of all vixens which would require sterilisation in order to nullify compensatory re-production. With pairs of foxes, the effect should be linear. If half of the vixens are sterilised, then half the cubs might be expected in a breeding season. However, as the number of vixens per group is increased, the proportion required to be sterilised to achieve the same reduction in births increased. For five vixens, over 80% of vixens needs to be sterilised. Since that may be difficult to achieve, immuno-contraception should be most effective at low populations.

## 4.2. Experiments on social control of breeding in captivity (A. Newsome & L. Hinds unpubl.)

That subordinates may breed when dominant vixens are surgically sterilised was tested on captive groups in large pens. In Year 1, four pens were 45×25m, and two others, 100×25m, with 10m buffers between all pens. In Year 2, the larger pens were subdivided into two more smaller ones to make eight of even size. Each pen was seeded with four individually collared sub-adult vixens and a sub-adult dog fox, all having been caught wild as cubs and reared in small groups of 6 to 8. In Year 1, the reproductive responses of subordinates in the different sized pens was examined without sterilising dominants. In Year 2, new pens were seeded with high-ranking subordinates from the first experiment, with extra newly caught and reared sub-adults making up the complements in all pens. After hierarchies were established, dominants were sterilised in four pens chosen randomly, with dominants in the other four being sham operated. Sterilisation was by surgical ligation and cauterisation of Fallopian tubes. Food was always in excess, and there were three large nesting boxes per pen, each with three

merged their litters within one den. One vixen attempted to raise a litter by herself, but insufficient food was brought to cubs which were harassed most by dog foxes None of the cubs survived. Those observations indicate that the dog fox in the pair may be important in provisioning and defence of the den.

A special aspect of the environment which might explain the sharing of resources and the high densities is that home ranges during the foxes' breeding season were separated from the food supply. Despite El Niño, the adult population on Round Is. remained high which implies adequate alternative food in winter. In Australia, the end of summer is likely to be the time of low food supply, and during droughts.

## 4. Experiments on social control of breeding in Australia

Experiments were conducted in pens to test whether or not dominance hierarchies remain stable and subordinates breed in compensation when dominants are sterilised surgically (see below). The concept was first examined mathematically.

entrance holes (though mostly the foxes camped in the open). Foxes were caught and weighed monthly, examined for reproductive activity, and blood taken for hormone assays.

Dominance hierarchies were identified utilising the interpretations and published figures from the captive studies of Tembrock (1957) and Macdonald (1977). Behaviours and interactions including any mating, denning or maternal behaviours were observed from hides using normal white light initially. Red light was then used as foxes became wary, and finally infrared light with video-taping. Preliminary results from plasma progesterone concentrations in the blood indicated that, regardless of treatment, high ovulation rates prevailed in both years, which could be expected from studies in the wild (Englund 1970, Lindström 1988). There was, however, little external sign (swollen vulvae) of oestrus, and no mating behaviour was seen in the pens. During whelping, pens were searched daily, and recorded fecundity was low. Only eight litters were found from 42 vixens in both years, and only one of them survived. That litter was born to a high status vixen in the first year of the study. Four subordinate vixens had litters, two of them in the one pen where the dominant had also whelped, and one of them in a pen with a sterilised dominant. The social relationships between that dominant and the subordinate mother plus the father were studied by Jenkins (1994). The indications were that the subordinate mother gained some protection from the dog fox which also provisioned the mother (see Birchfield 1980 also), but the cubs were found half eaten at 3 weeks of age.

The studies indicate no loss of dominance with sterilisation, and no compensatory breeding in their subordinates. Pen effects were obvious, resulting in loss and killing of cubs. The high early reproductive rate may be attributable to abundant food on the one hand, and the ultimately poor productivity, to confinement and hierarchical interactions. Final results will be published in detail elsewhere. Meanwhile, studies of the impact on social structures and reproduction of surgical sterilisation have begun in the field as mimics of immuno-sterilisation. The first field trial commenced in 1991 in Kosciusko National Park and is being written up (Bubela

unpubl.), and a more extensive experiment was established in 1994 on replicated areas (J. McIlroy & G. Saunders in prep.). Associated with it is a study of mortality rates in rabbits (*Oryctolagus cuniculus*) and brush tailed possums (*Trichosurus vulpecula*) under different treatments of fox removal (D. Hik & A. Newsome in prep.).

# 5. Discussion

What does this mean for the red fox in Australia and for the control of populations especially by immuno-contraception on the broad-scale? The studies examined here from Alaska and Sweden were chosen especially because they show the degree of flexibility possible in wild populations of red foxes as food supplies change. The Swedish studies show that extra vixens on home ranges may breed, but resorption in utero and poor survival of cubs dampens population increase even when there is sufficient food. The concern here, indicated by the models of Caughley et al. (1992), is that immuno-contraception may lessen that damping effect. Theoretically, that should not happen, because hormonal systems should remain functional. Thus, the conservative hypothesis is indicated for the red fox in Australia, that the key facets of its demography, reproduction, and social complexities (including territoriality) will change according to whether drought or plenty prevails. Thus, during eruptions of rabbits, group living may arise, high fecundity, including breeding among subordinate vixens, and improved survival rates of their young, but whether mean litter size will vary requires study. The Australian pen studies reported here support the prospect of facultatively high rates of ovulation at high food supplies as in Sweden (Englund 1970, Lindström 1991) (see above); but recruitment was low due to social interference and crowding. Bakken's (1991) study of highly variable reproduction in farmed silver red foxes (*Vulpes vulpes*) in Norway showed that poor survival of cubs was associated with social status. Fecundity and survival of cubs declined markedly if low ranking vixens where placed alongside those of high ranking, despite being in separate cages.

When food runs short in the wild, however, social systems should simplify, with groups dissolving to pairs and even loners, with reproduction low and foxes dispersing. The few studies of wild fox populations from Australia indicate overlap and infidelity in the use of home ranges (Marlow 1992), excursions from home ranges (Coman et al. 1991, Marlow 1992), and co-operative scent-marking, food retrieval for cubs. In areas where rabbits are uncommon, patterns of low, dispersed populations of foxes may prevail (P. Thompson & N. Marlow in prep.) e.g., as in semi-arid regions. There, fox demography can be expected to vary between formation of groups and their collapse depending on whether rabbits are eruptive or not. The mechanisms for such change are not clear, whether they are passive or active on the part of the foxes.

Another concern with immuno-contraception is that territorial defence may not always be of outer limits of home ranges. In an Australian study (Birchfield 1980), defence was of hunting areas but they were within home ranges. It was limited to dens on Round Is. (Zabel & Taggart 1989), where home ranges did not include the food supply which was a shared resource for a high population of foxes (see Sargeant 1972, Voigt & Macdonald 1984, Mulder 1985). Boitani et al. (1984) found foxes living on the hillsides but scavenging in the valleys for food. Movements outside home ranges are sometimes termed 'excursions' but, as above, may be for other purposes including mating. The point is that such movements represent social flexibility also.

The evolutionary theories on group formation in the red fox were mentioned in the Introduction: the Resource Dispersal Hypothesis (Macdonald 1983, Carr & Macdonald 1986), the Constant Territory Size Hypothesis (von Schantz 1984) and the Territory Inheritance Hypothesis (Lindström 1986). Such theories can hardly ever be tested, but Lindström provides testable hypotheses on instability of groups as they increase in size. Another testable issue concerns the role of 'helpers' within groups. The concept of co-ordinated territorial drift in red foxes (Doncaster & Macdonald 1991) might be difficult to test, however, especially to identify mechanisms which provide such a degree of organisation and flex-ibility and which operate beyond individual home ranges or territories.

Thus, no general theory for the fox's social system has arisen, except, perhaps, that none is as yet achievable. The statement that theory has outstripped empirical data (Bekoff et al. 1981) remains true for the red fox today. Stamps (1994) has argued that current perceptions for territorial animals are underlain by untested assumptions which have become accepted verities (see her Table 1). That author argues that territory formation may not be all about acquisition of food resources (see Zabel & Taggart 1989), and that observed variables such as size of the animal, its experience, habitat selection and territorial behaviour, may be correlates with causative factors which do confer fitness. Further, the philosophical shift from earlier comparative studies of territoriality to an economic approach has resulted in distortion, with some environmental and social factors now being ignored, e.g., over-dispersion may offset problems due to predation and pathogens rather than be territorial responses. Models may assume that encounters are independent of one another, but neighbours may encounter one another repeatedly during tenure of territory (Stamps 1994, p. 216), just as they meet subordinates, supernumerary foxes or 'floaters' and so learn about the social and physical environments.

## 6. Conclusions

The issues of ultimate causes and proximal outcomes of sociality in red foxes remain a challenge. Because group living in red foxes does not involve group hunting to acquire food, perhaps it is the niche requirements which have allowed the evolution of so flexible a social system. Of use in understanding may be Hutchinson's (1951, 1961) term 'fugitive species'. It was adopted by Voigt and Earle (1983) to describe the way in which the red fox lives with the coyote (*Canis latrans*), essentially in the interstices between coyote ranges, so avoiding them. Unravelling the problem for the red fox in an adopted land, Australia, where the species poses major problems for wildlife conservation, is essential for immuno-contraception to be effective as a means of broad-scale population control.

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