



Original investigation

## Costs of reproduction—A demographical approach to examine life-history trade-offs in two old-world deer species

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## ABSTRACT

Resource-allocation trade-offs comprise fundamental constraints on life-history evolution. In particular, the trade-offs between reproduction and longevity and between present and future reproduction are believed to be important in shaping reproductive patterns. Unfortunately, exploring such trade-offs in natural populations is complicated and may not be possible in all taxa. Against this background we here use zoo data for enhancing our understanding of reproductive patterns in two endangered and cryptic deer species (Vietnamese sika deer *Cervus nippon pseudaxis*, Mesopotamian fallow deer *Dama dama mesopotamica*). In both species, births peaked right before the onset of the rainy season in the species' natural environments. Females reached high reproductive output earlier in life and had (in one species only) higher survival rates than males. Offspring number covaried positively rather than negatively with longevity. In females, the length of the reproductive phase correlated positively with longevity, birth rate within the entire lifespan, and offspring number, while it was negatively related to the birth rate during the reproductive phase (in 1 species). The length of the post-reproductive phase was positively related to longevity and negatively to the birth rate during the entire lifespan. Taken together, we revealed several patterns being presumably of ecological relevance including indications for trade-offs among offspring quality and quantity, and between present and future reproduction even within these captive populations relieved from seasonal (e.g. food) constraints. In spite of some limitations, our study reconfirms that zoo data offer insights into the reproductive biology of species for which field data are difficult to obtain.

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## Introduction

Life histories describe the life cycles of organisms in an evolutionary or comparative context, based on the notion that differences have been shaped by natural selection (Roff, 2002; Stearns, 1989). Therefore, life-history traits such as age at first reproduction, number and quality of offspring, parental care, and longevity are considered to be ecologically important (Roff, 2002; Stearns, 1989; Williams, 1966; Zera and Harshman, 2001). In order to maximize fitness, organisms should ideally behave like the 'Darwinian demon', i.e. they should start reproducing an unlimited number of offspring directly after birth until eternity (Stearns, 1989; Williams, 1966). However, such an organism does not exist, basically because of (energetic) constraints (Stearns, 1989). In reality, organisms have to weigh the costs and benefits of an investment into each

individual trait, as the energy allocated to a specific function is not available to other functions anymore. The resulting resource-allocation trade-offs comprise the principal life-history challenge, as improving one trait is predicted to have negative effects on others (Roff, 2002; Stearns, 1989; Zera and Harshman, 2001). Such trade-offs are thought to comprise fundamental constraints on life-history evolution (Bell and Koufopanou, 1986; Clutton-Brock et al., 1983; Williams, 1966).

Apart from offspring production, longevity is, at least in long-lived, iteroparous species an important factor affecting individual fitness, as it frequently correlates in a positive manner with reproductive output (Clutton-Brock, 1988; Newton, 1989; Stearns, 1989; Zera and Harshman, 2001). On the other hand, an increased energy allocation into reproduction has been repeatedly found to be traded off against longevity (Roff, 2002; Stearns, 1989; Zera and Harshman, 2001). Thus, predictions regarding the relationship between lifespan and reproductive investment are challenging as outcomes are likely to be affected by specific parameters, for instance food availability, body size and storage reserves, to which lifespan is often positively related (Roff, 2002). The total lifespan of an organism can be divided into the pre-reproductive, reproductive and post-

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reproductive phase (Promislow, 1992; Rose, 1991). This may be especially important in long-lived species, which may not be reproductively active during a large proportion of their lifespan.

Apart from potential trade-offs between reproduction and longevity, another ‘classical’ trade-off is the one between present and future reproduction, stating that an increase in present reproduction can only be achieved at the expense of reduced future reproduction opportunities (Roff, 2002; Stearns, 1989). Such trade-offs are often modulated by population density. High densities typically result in reduced feeding and storage reserves, and increased susceptibility to parasites and diseases, jointly reducing reproductive potential (Clutton-Brock and Guinness, 1982; Forchhammer et al., 1998; Stewart et al., 2005). To alleviate negative effects of energetic constraints, the timing of giving birth is typically synchronized with the periods of highest food availability, combined with favourable climatic conditions, in natural populations (Lincoln, 1985; Zerbe et al., 2012).

When investigating trade-offs associated with reproduction, one should ideally score the life-time reproductive success from large-scale datasets along with longevity in wild populations. However, such studies are difficult to conduct due to high concomitant expenses in terms of costs and time (Clutton-Brock and Guinness, 1982; McElligott and Hayden, 2000). We therefore make here use of zoo records which are laid down in so-called studbooks, including detailed information on longevity and offspring production for each individual (e.g. Pelletier et al., 2009; Rudloff, 1991–2013; Rudloff, 1994–2013). In particular, we used two data-sets of old-world deer species (Mammalia, Artiodactyla, Cervidae), namely the Vietnamese sika deer (*Cervus nippon pseudaxis* Eydoux and Souleyet, 1841) and the Mesopotamian (Persian) fallow deer (*Dama dama mesopotamica* Brooke, 1875). Both species are endangered and subject to reintroduction projects (Bar-David et al., 2005; Ratajszak et al., 1993; Saltz et al., 2011). This study may therefore additionally help to better understand their reproductive behaviour in captivity, knowledge which may prove important to increase offspring production for reintroductions.

Specifically, we here set out to answer the following questions: (1) Does population density affect vital (birth and death) rates? (2) Do births show age-specific and seasonal patterns? (3) Are there sex differences in survival patterns which may reflect differential investment into reproduction? (4) Are reproduction and longevity traded-off against each other or are they positively correlated? (5) Do patterns differ if considering reproductive versus non-reproductive phases?

## Material and methods

### Study organisms

*C. n. pseudaxis* is native to Vietnam where it inhabits woodland within the temperate-zone region (Nowak, 1999; Ratajszak et al., 1993). Mating occurs in autumn and gestation lasts for about 210–223 days (Haensel, 1980; Nowak, 1999; Puschmann, 2003). *C. n. pseudaxis* is considered extinct in the wild, but captive populations still exist for the production of velvet (Nowak, 1999; Whitehead, 1993). The European ex situ population of the taxon was imported from Ha-Tinh and Cuc Phuong (Haensel, 1980; Rudloff, 1991–2013). The basis of founders is relatively broad, though most animals originate from one site (Ratajszak et al., 1993; Thévenon et al., 2003).

Fallow deer live in a variety of climates ranging from cool-humid to warm-dry areas (Chapman and Chapman, 1980; Haltenorth, 1959; Nowak, 1999; Saltz et al., 2011). *D. d. mesopotamica* formerly occurred in Iran, Iraq, Israel, Jordan, Lebanon, Palestine, Syria, and eastern Turkey (Chapman and Chapman, 1980; Nowak, 1999). Fol-

**Table 1**

Summary of parameters (including categories/units) used to investigate life-history patterns in *Cervus nippon pseudaxis* and *Dama dama mesopotamica*.

Parameter	Categories/units
Sex	male, female
Longevity	[days]
Density	Number
Age at first reproduction	[days]
Length of reproductive phase	[days]
Length of post-reproductive phase	[days]
Offspring number	Number
Offspring number surviving > 100 days	Number
Birth rate per year throughout the entire lifespan	[number/year]
Birth rate per year throughout the reproductive phase	[number/year]

lowing severe population declines, the taxon is nowadays highly endangered and restricted to a small number of protected sites only (Chapman and Chapman, 1980; Jantschke, 1991; Saltz et al., 2011). The zoo population of *D. d. mesopotamica* has been founded by only three individuals – two males and one female (Haltenorth 1959; Jantschke, 1991; Puschmann, 2003). Fallow deer females usually give birth to only one offspring after a gestation period of approximately 229 days (Nowak, 1999; Puschmann, 2003). Both deer species are polygynous, sexually dimorphic and have a similar reproductive pattern. In the breeding season, male deer establish and defend territories, which are visited by females. Females typically copulate exclusively with the dominant male (Clutton-Brock and Guinness, 1982; Lincoln, 1985; Nowak, 1999).

### Data acquisition and analyses

Because of their high endangerment, the World Association of Zoos and Aquaria decided to establish international studbooks for both deer species, starting in 1992 (*C. n. pseudaxis*; Rudloff, 1991–2013) and 1994 (*D. d. mesopotamica*; Rudloff, 1994–2013), respectively. The studbooks contain information on sex, date of birth, date of death, identity of father and mother, transfer dates, and keeping places for all individuals kept in zoos at the global scale. These data form the basis of all subsequent analyses. Only individuals that had already died were considered. We selected the first 700 registration numbers of *C. n. pseudaxis* and the first 500 registration numbers of *D. d. mesopotamica*. From these we excluded individuals (1) from populations in which contraception or culling was applied, (2) from the southern hemisphere as they have to adapt to different light cycles and climatic conditions which may affect vital rates, and (3) for which both parents were unknown (i.e. at least one parent was known). In total 396 *C. n. pseudaxis* and 188 *D. d. mesopotamica* fulfilled the above mentioned criteria. The data contained in the studbooks were used to compile a variety of variables for these animals (Table 1). In addition to the individual-based data mentioned in Table 1, the following population-level variables were calculated: number of individuals (males or females) at the beginning of a year per keeping (=population density), annual natality (number of births/number of females) and annual mortality rate (number of dead individuals/number of individuals; cf. Table 2). Furthermore, we calculated ‘individual density’ as the mean group size experienced by a given individual during its entire life span. We finally scored the mean longevity of offspring for all females for which at least 50% of offspring longevities were available.

### Statistical analyses

All statistical tests have been computed using SPSS 13.0 or Minitab 16. The distribution of births in relation to age of both sexes (Fig. 1) and to season (time of year; Fig. 2) were tested against each other using the Kolmogorow-Smirnow test. Survival curves

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