

Corey J. A. Bradshaw · Robert G. Harcourt ·  
Lloyd S. Davis

## Male-biased sex ratios in New Zealand fur seal pups relative to environmental variation

Received: 3 June 2002 / Revised: 15 December 2002 / Accepted: 12 January 2003 / Published online: 25 February 2003  
© Springer-Verlag 2003

**Abstract** A number of models have been proposed to provide adaptive explanations of sex-ratio variation in mammals. Two models have been applied commonly to primates and ungulates with varying success – the Trivers-Willard (TW) hypothesis, and the local resource competition (LRC) hypothesis. For polygynous, sexually dimorphic mammals, where males are larger and disperse more readily, these models predict opposite outcomes of sex-ratio adjustment within the same environmental context (high-resource years: TW – more sons; LRC – more daughters). However, many of the predictions of these two models can vary depending on factors influencing resource availability, such as environmental stochasticity, resource predictability, and population density. The New Zealand fur seal (*Arctocephalus forsteri*) is a polygynous mammal showing marked sexual dimorphism (larger males), with higher variation in male reproductive success expected. We provide clear evidence of male-biased sex ratios from a large sample of *A. forsteri* pups captured around South Island, New Zealand during 1996/1998, even after accounting for a sex bias in capture probability. The extent of the bias depended upon year and, in 1998, strong climatic perturbations (El Niño/Southern Oscillation, ENSO) probably reduced food availability. Significant male-biased sex ratios were found in all years; however, there was a significant decline in

the male bias in 1998. There was no relationship between sex ratio and population density. We suggest that the sex-ratio bias resulted from the production of relatively more male pups. Under the density-independent scenario, the strong male bias in *A. forsteri* sex ratios is support for the TW model within an environment of high resource predictability. We suggest that some plasticity in the determination of pup sex among years is a mechanism by which *A. forsteri* females in New Zealand, and perhaps other otariid seals, can maximise fitness benefits when living in regions of high, yet apparently predictable, environmental variability. We also suggest that much of the inconsistency in the reported sex ratios for otariid seals results from the complex interaction of population density and environmental stochasticity influencing relative food availability over time.

**Keywords** Pup sex ratios · *Arctocephalus forsteri* · Environmental variability · Trivers-Willard hypothesis · Local resource competition

### Introduction

It has long been argued that equal sex ratios are evolutionary stable because parental investment in sons and daughters should, assuming stable local environments (Frank 1990) and population-wide random mating (Cockburn et al. 2002), be equal (Fisher 1930). However, the sex ratio of vertebrate offspring can vary due to a range of factors including nutritional stress, age, condition, and social rank of mothers, litter size, population density and changes in resource availability (Clutton-Brock and Iason 1986; Dickman 1988; Hardy 1997; Dittus 1998; Cameron et al. 1999; Kruuk et al. 1999; Cameron and Linklater 2000; Packer et al. 2000; Côté and Festa-Bianchet 2001; Byholm et al. 2002; Johnson and Ritchie 2002). Discussion on the adaptiveness of sex-ratio variation focuses on the idea that parents should adjust the sex ratio of offspring in response to factors affecting their own and their offspring's future reproductive success (Clutton-

Communicated by F. Trillmich

C. J. A. Bradshaw (✉)  
Antarctic Wildlife Research Unit, School of Zoology,  
University of Tasmania,  
G.P.O. Box 252-05, Hobart, Tasmania 7001, Australia  
e-mail: corey.bradshaw@utas.edu.au  
Tel.: +61-3-62262644  
Fax: +61-3-62262745

R. G. Harcourt  
Marine Mammal Research Group,  
Graduate School of the Environment,  
Macquarie University,  
Sydney, New South Wales 2109, Australia

Brock et al. 1984; Hewison et al. 1999). However, the evidence for this in vertebrates is not always convincing because vertebrates appear to have a limited capacity for adaptive control of the primary sex ratio (Williams 1979; Packer et al. 2000; Cockburn et al. 2002).

A number of models have been proposed to provide adaptive explanations of sex-ratio variation in mammals and birds (see Cockburn et al. 2002 for review). The most influential model applied to sex-ratio variation in mammals predicts that in polygynous species with marked sexual dimorphism, mothers in good (body) condition will invest in the sex showing the highest variation in reproductive success (Trivers and Willard 1973; Maynard-Smith 1980; Charnov 1982). This is because investment in that sex can potentially provide a better return on maternal investment in terms of future reproductive success (Maynard-Smith 1980; Clutton-Brock 1982). This, the Trivers and Willard (TW) model (Trivers and Willard 1973), predicts that mothers in better condition should bias their investment toward offspring of the sex that can provide the best return on investment, even though such investments are riskier. While the large reproductive asymmetries typically associated with the male sex mean that the rewards are potentially greater for a mother producing a son, the risk of failure is also greater. This is because for every successful male there will be many that do not succeed. Because the condition of males is often a predictor of their future reproductive success, mothers in good condition that are capable of investing heavily in their sons increase the probability of future returns.

Thus, for a given unit of maternal investment by a high-quality mother, the reproductive value of sons and daughters will be different (Cockburn et al. 2002). There is evidence to support this prediction in some mammalian species (Clutton-Brock et al. 1981; Austad and Sunquist 1986; Clutton-Brock and Iason 1986; Gosling 1986; Rutberg 1986; Dickman 1988; Kojola and Eloranta 1989; Arnbohm et al. 1994; Dittus 1998). In the case of polygynous mammals with larger males, this model assumes that: (1) male reproductive success is more variable than that of females, and thus, males may be more strongly affected by physical (body) quality, (2) physical quality (e.g. body size) of adult males depends on the physical quality at the end of maternal care, and (3) mothers in good physical condition are better at caring for their young than mothers in poor physical condition (Hewison et al. 1999).

An alternative theoretical model of adaptive sex ratio predicts an opposite bias in offspring sex ratios for polygynous mammals where larger males have a greater variation in reproductive success. This is known as the local resource competition (LRC) model (Clark 1978; Silk 1983), and it predicts that mothers in poor condition should produce the sex more likely to disperse from the natal area because the non-dispersing sex is more likely to compete for local resources with the parents. Thus, in many mammal species where males are the main dispersing sex and females are more philopatric, mothers

in poor body condition are predicted to produce more sons on average (Hewison et al. 1999).

When sex-ratio biases are observed, the behavioural, sociobiological, demographic and environmental contexts of the species under study must be understood before any particular model can be applied to explain the bias (Krackow 1997). For example, the degree of co-operation between offspring and parents, the sex-specific dispersal capability of the offspring, habitat heterogeneity (Julliard 2000; Byholm et al. 2002) and environmental (resource) predictability (West and Sheldon 2002) must all be quantified or, at least, understood before an adequate interpretation can be made. Further, Hewison et al. (1999) argued that special attention must be paid to the assumptions underlying each model before testing the adaptiveness of sex-ratio bias in particular species or populations.

Otariid seals (fur seals and sea lions) provide good test species for the application of models to sex-ratio adaptation because they are monotocous and breed once annually (Gentry and Kooyman 1986). Further, males do not participate in the care of offspring, all species are highly polygynous (Bartholomew 1970; Bradshaw et al. 2000a), and all are highly sexually dimorphic with adult males weighing much more than adult females (Bartholomew 1970). There is some evidence that the birth mass of sons, but not daughters, is limited by the mother's mass and body condition (Boyd and McCann 1989, although see Trillmich 1996 for a discussion of conflicting results). Further, there is evidence for a higher in utero energy allocation to sons than to daughters (Georges and Guinet 2001), and that birth size influences growth rates and survival (Calambokidis and Gentry 1985; Boltnev et al. 1998; Georges and Guinet 2000a, 2000b). Finally, individual measurements such as body mass and condition, and demographic parameters such as population density, can be determined with relative ease for a large number of individuals and populations (e.g. Trites 1993; Bradshaw et al. 2000a).

In the income-breeding (sensu Boyd 2000) otariids, there is conflicting evidence on the existence of sex-ratio bias, with some authors finding even ratios at birth or shortly thereafter (Bonner 1968; Boyd and McCann 1989; Goldsworthy and Shaughnessy 1994; Georges and Guinet 2000a, 2001), and others finding male-biased ratios (Rand 1956; Trillmich 1986; Oosthuizen 1991; Trites 1991; Shaughnessy 1993; Antonelis et al. 1994; Ono and Boness 1996; Lunn and Arnould 1997; Goebel and Calambokidis 1998; Mison-Jooste 1999). The applicability of pinnipeds to the TW model has been questioned previously (Trillmich 1996), and recent discussions on the evolution of sex-ratio adjustment have made the interpretation of previous results less conclusive (Krackow 1997; Hewison et al. 1999; Julliard 2000; Cockburn et al. 2002; West and Sheldon 2002). Further, it is not clear, even when biases occur, what physiological mechanism(s) exist for the differential production of one sex versus the other (Arnbohm et al. 1994; West and Sheldon 2002).

A possible confounding factor in the interpretation of otariid offspring sex-ratio adjustment under the TW model is the suggestion of differential dispersal capability between males and females. Although data describing juvenile dispersal and adult philopatry are not complete, most sources suggest that male otariids have a greater dispersal capacity than females (Oosthuizen 1991; Boyd et al. 1998), and that females generally demonstrate greater philopatry (Lunn and Boyd 1991; Bradshaw et al. 2000b). Another confounding factor in the LRC model of differential dispersal is the effect of heterogeneity in habitat quality leading to different outcomes in sex-ratio adjustment. When species that live in heterogeneous environments have sex-biased dispersal, biases in offspring sex ratio will tend toward the more dispersing sex in poor-quality habitats, and toward the more philopatric sex in good-quality habitats (Julliard 2000). Indeed, there is evidence for geographic variation in the dispersal capacity of fur seals (Bradshaw et al. 1999).

West and Sheldon (2002) recently proposed that environmental (resource) predictability will lead to weaker selection for sex-ratio adjustment. They suggested that if environmental factors (e.g. food availability) are not predictable, then skewed sex ratios may lead to chance overproduction of the sex with the lowest reproductive value (West and Sheldon 2002). In otariid seals, adverse environmental conditions have led to female-biased sex ratios. Both California sea lions (*Zalophus californianus*) and Galapagos fur seals (*Arctocephalus galapagoensis*) have shown female-biased sex ratios in years when resources were limiting (Trillmich 1986; Francis and Heath 1991; Ono and Boness 1991), which is consistent with the prediction that male offspring will have either higher abortion rates in utero (Ono and Boness 1991) or higher post-partum mortality (Arnbom et al. 1994) when the condition of mothers decreases substantially.

A further complication to the influence of a variable environment on mammalian sex ratios is the facultative influence of population density on physical quality. In high-density ungulate populations, there is no evidence for male-dominated sex ratios under the TW hypothesis (Kruuk et al. 1999), suggesting this may be a general phenomenon (Cockburn et al. 2002). Indeed, many population parameters covary with population density in otariids (Doidge et al. 1984; Fowler 1990; Bradshaw et al. 2000a), especially in situations of reduced food availability (Bradshaw et al. 2000a). Therefore, a complex interaction of selective pressures on adaptive variation in otariid sex ratios is hypothesised to occur within a given breeding season: environmental quality, environmental predictability, habitat heterogeneity and population density.

In this paper, we present the sex ratios of New Zealand fur seal (*A. forsteri*) pups from a relatively large sample collected in the first few months following parturition over 3 years around South Island, New Zealand. The New Zealand population of *A. forsteri* is recovering from severe overexploitation in the nineteenth century, with

many colonies increasing rapidly (ca. 20–25% annually, Lalas and Bradshaw 2001). New Zealand fur seals come ashore to breed in colonies from mid-November to early January (austral summer), with mean pupping in mid- to late December (Mattlin 1987; Lalas and Harcourt 1995). Mothers give birth to a single pup and remain with it for a mean of 9 days before returning to sea to feed (Harcourt et al. 1995). Mothers alternate between foraging trips at sea and time ashore to suckle pups until pups are weaned at approximately 10 months of age (Mattlin 1987).

This study coincided with two El Niño-Southern Oscillation (ENSO) events: a weak La Niña (1996) and strong El Niño (1998) (Basher 1998; Bradshaw et al. 2000a). During El Niño years, New Zealand receives more frequent westerly winds during summer leading to more rain in the west and drought conditions in the east. In winter, El Niño results in dominant southerly winds that bring colder terrestrial and oceanic conditions (Basher 1998). La Niña events have weaker impacts on the New Zealand climate, resulting in more northeasterly winds that bring rainy conditions to the northern regions of New Zealand (Basher 1998). Because the effects of ENSO events in New Zealand are generally less extreme and possibly more predictable than in other regions (Basher 1998; Trillmich and Kooyman 2001), we hypothesise that this higher relative predictability in resource availability may lead to a sex-ratio skew. Specifically:

1. In high-resource years and when population density is low:
  - a. the TW model predicts a higher production of male pups, and
  - b. the LRC model predicts a higher production of female pups.
2. In poor-resource years:
  - a. the TW model predicts a reduction in the production of male pups, and
  - b. the LRC model predicts a higher production of males.

We discuss our results within the context of the most appropriate adaptability model(s) and their predictions, and focus on the influence of environmental variability and population density on sex-ratio adjustment in otariid seals.

---

## Methods

We investigated 16 (1996), 19 (1997) and 20 (1998) breeding colonies of New Zealand fur seals around South Island, New Zealand (Bradshaw et al. 2000a). Pups were caught after the pupping season from 3 January to 3 March; thus pups ranged in age from approximately 10–69 days when caught (median pupping date is 24 December, Lalas and Harcourt 1995). We caught pups at random by hand or with a noose pole in the breeding colonies studied. All pups were weighed to the nearest 0.1 kg (Bradshaw et al. 2000a) using a 20-kg balance (Pesola, Baar, Switzerland). Sample sizes were typically large relative to the population of pups in each colony (mean=53.8%, Bradshaw et al. 2000a).

For all estimates of sex ratio, we removed colonies with <20 pups of either sex to avoid potential bias due to low sample size. Previously, it has been reported that biases in the reporting of sex ratios can be related to sample size (Palmer 2000; Johnson and Ritchie 2002; West and Sheldon 2002). To investigate the variation in sex ratios per colony relative to sample size, we regressed pup sex ratios (sampled and mass-adjusted proportion of males; see below) against sample size (number of pups caught per colony) using randomised, linear regression (20,000 randomisations, Manly 1997). We also regressed pup sex ratios (sampled and mass-adjusted proportion of males; see below) with sampling date to determine if there was a bias associated with sampling date using randomised, linear regression (Manly 1997).

Further, it has been suggested that observed biases in sex ratio may result from differential probabilities of capture between the sexes (Buskirk and Lindstedt 1989; Gehrt and Fritzell 1996). Although capture probability does not differ between the sexes in *A. forsteri* pups, it does vary with body size; larger pups have a lower probability of capture (Bradshaw et al. 2003). Thus, we investigated whether the sex ratio of pups varied according to mass. Pups were divided into three, uniform mass classes: "light" (0<mass≤6.8 kg), "medium" (6.8<mass≤9.0 kg) and "heavy" (mass>9.0 kg), following the procedure outlined in Bradshaw et al. (2003). We used a *G*-test with William's correction (Sokal and Rohlf 1981) to identify any differences in sex ratio among mass classes per year, and for all years combined.

We then adjusted the observed numbers of male and female pups for analysis, and we present all subsequent analyses of observed and adjusted sex ratios for comparison. We estimated the number of individuals within each group that would have been captured with uniform capture probability of 1.0 across mass classes. To do this, we used the estimated capture probabilities ( $\hat{p}$ ) for each mass class as estimated from a large sample of pups captured ( $n=719$  pups tagged) from 3 colonies (FG, SMN and TKS, Table 1) over 2 years by Bradshaw et al. (2003). Differential capture probability was estimated using a multi-state mark-recapture model (Nichols et al. 1992) where mass state ("light", "medium" and "heavy") was incorporated into a modified Jolly-Cormack-Seber mark-recapture model (1,650 separate estimates of mass) to account for pups missed during capture sessions. Bradshaw et al. (2003) found strong evidence for a dependence of capture probability on mass state: "light":  $\hat{p} = 0.873 \pm 0.081$  ( $\pm$ standard error), "medium":  $\hat{p} = 0.664 \pm 0.042$ , and "heavy":  $\hat{p} = 0.540 \pm 0.026$ . Therefore, the adjusted number of individuals in each group became:

$$\hat{N}_r = \frac{n_r}{\hat{p}_r}$$

where  $n_r$ =number of individuals in mass class  $r$ , and  $\hat{p}_r$ =estimated capture probability for mass class  $r$ . The standard error of  $\hat{N}_r$  is:

$$\widehat{SE}(\hat{N}_r) = \frac{n_r \left[ \widehat{SE}(\hat{p}_r) \right]}{(\hat{p}_r)^2}$$

The ratios of males to females captured at each colony were examined to test the hypothesis of equal sex ratios. We used a *G*-test with William's correction (Sokal and Rohlf 1981) to identify any significant departure from a 1:1 sex ratio, which is also shown when the lower 95% binomial confidence interval limits for the proportion of male pups exceed 0.5. To determine the effect of year and colony on pup sex ratios, we fitted four logistic regression models to the data, where the number of male and female pups were grouped according to natal colony (*colony*) and sampling year (*year*). Model selection was based on Akaike's Information Criterion (AIC; Lebreton et al. 1992), with the best model having a low AIC value and a high model weight calculated from the differences in AIC (Buckland et al. 1997).

Pups of *A. forsteri* in New Zealand demonstrate a small difference in the probability of survival between males and females (Bradshaw et al. 2003). Because the date of pup capture at each colony was not the same in the period following the breeding season (Table 1, Bradshaw et al. 2000a), we examined whether the

small difference in survival probability ( $\hat{S}$ ) between the sexes could have altered the observed and adjusted sex ratios further. Sex-specific probabilities of survival were estimated as the mean from 3 colonies on Otago Peninsula, South Island, New Zealand over 2 years (i.e. colonies FG 1997, FG 1998, SMN 1998 and TKS 1998, see Table 1), during a 47-day interval:  $\hat{S}_{female} = 0.942 \pm 0.033$ ,  $\hat{S}_{male} = 0.967 \pm 0.019$  (Bradshaw et al. 2003). We compared the capture probability-adjusted numbers of pups of each sex with and without taking differential survival into consideration by first calculating the proportion of the 47-day interval that had elapsed from immediately post-pupping to the time of sampling at each colony. The interval ( $t$ ) survival probability of sex  $g$  is:

$${}_g\hat{S}_t = {}_g\hat{S}^{(t/47)}$$

The number of animals within each sex and mass class adjusted for differential probability of survival between the sexes became:

$${}_g\hat{N}_r = \frac{\hat{N}_r}{{}_g\hat{S}_t}$$

After adjusting for differential capture probability on the numbers of females and males in each sample, no significant change occurred to these adjusted numbers when accounting for differential survival probability between the sexes (1996:  $G_1=0.03$ ,  $P=0.865$ ; 1997:  $G_1=0.19$ ,  $P=0.663$ ; 1998:  $G_1=0.04$ ,  $P=0.841$ ). Therefore, for all analyses we used the number of individuals within each sex adjusted for capture probability only. This also avoided any issues associated with not having colony-specific survival probabilities for all colonies sampled.

Sampling at all colonies had associated pup density estimated at date of capture (Bradshaw et al. 2000a); therefore, we examined if there was any influence of pup density on the sex ratio at each colony using randomised, linear regression (Manly 1997).

## Results

After removing the colonies with <20 pups per sex, the number of colonies used in the analyses were 10 (1996), 16 (1997) and 16 (1998). The total sample of pups caught in these colonies was 4,549 (2,394 males and 2,155 females; Table 1).

Plotting the proportion of male pups (original and mass-adjusted samples) against sample size ( $\log_{10}$  number of pups caught per colony) revealed no apparent trends (Fig. 1), and there were no significant relationships based on 20,000 randomisations (unadjusted:  $P_{20,000}=0.104$ , Fig. 1a; mass-adjusted:  $P_{20,000}=0.100$ , Fig. 1b). Thus, there is no evidence of selective bias based on sample size (Johnson and Ritchie 2002; West and Sheldon 2002).

Sampling date for each colony explained a small, but significant, proportion of the variation in the proportion of male pups captured ( $R_{adj}^2=0.092$ ,  $P_{20,000}=0.015$ , Fig. 2a). Using the mass-adjusted proportion of male pups per colony (see below), the variance explained by sampling date increased slightly ( $R_{adj}^2=0.122$ ,  $P_{20,000}=0.006$ , Fig. 2b). Due to the small influence of sampling date on sex-ratio estimates, and high pup survival reported for the first few months after parturition (ca. 0.9, Bradshaw et al. 2003), we conclude that the effect of sampling date on sex ratio is negligible.

For the observed data (i.e. not adjusted for differential capture probability), the proportion of males in each sample exceeded 0.5 in all years, expressed either as the

**Table 1** The samples of male and female pups captured per colony per year, the estimated pup density at each colony (Bradshaw et al. 2000a), and the associated sampling dates. Also shown are the mass-adjusted samples based on the capture probabilities for “light” ( $0 < \text{mass} \leq 6.8$  kg), “medium” ( $6.8 < \text{mass} \leq 9.0$  kg) and “heavy” ( $\text{mass} > 9.0$  kg) pups from Bradshaw et al. (2003). Colony abbreviations taken from Bradshaw et al. (2000a)

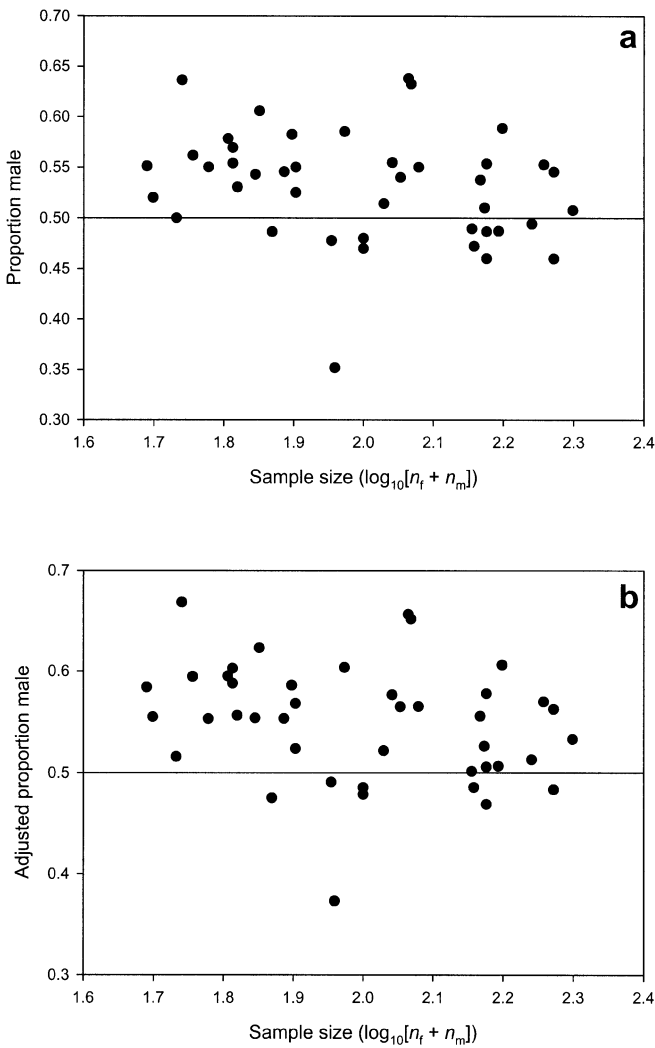
Year	Colony	Male:female unadjusted	Male:female adjusted	Pup density (pups/100 m <sup>2</sup> )	Sampling date
1996	BB	42:38	51:46	2.6	13/01/1996
	BIW	38:32	48:39	6.9	18/01/1996
	CF	35:20	48:24	10.4	03/02/1996
	FG	42:35	51:41	6.3	06/01/1996
	HB	36:29	57:40	3.8	25/01/1996
	OBI	46:33	58:41	5.8	07/02/1996
	SMN	33:27	40:32	6.7	06/01/1996
	TI	32:25	57:39	4.1	20/02/1996
	WEKN	27:22	38:27	7.7	31/01/1996
	WEKS	61:49	83:61	16.5	29/01/1996
1996 Total		392:310	531:390	$\bar{x}=7.1$	
1997	BB	76:80	101:99	2.8	17/01/1997
	BIW	102:85	166:129	8.7	01/03/1997
	CF	70:73	93:93	7.5	28/01/1997
	CHN	26:24	37:30	3.6	27/01/1997
	FG	68:76	88:93	8.4	06/01/1997
	HB	74:42	127:67	3.8	21/02/1997
	NUGN	43:28	57:35	14.3	11/01/1997
	OBI	101:98	138:121	6.1	03/02/1997
	OP	27:27	46:43	1.0	14/02/1997
	QBE	37:27	62:42	6.3	18/02/1997
	SMN	61:52	82:64	8.9	06/01/1997
	TI	44:36	69:53	5.7	11/02/1997
	TKS	55:39	71:47	10.2	06/01/1997
	VICN	32:59	44:74	5.6	09/01/1997
	WEKN	74:43	101:54	6.4	29/01/1997
	WEKS	79:68	104:83	14.3	27/01/1997
1997 Total		969:857	1386:1124	$\bar{x}=7.1$	
1998	BB	86:101	113:121	3.1	14/01/1998
	BIW	86:88	134:128	5.3	03/03/1998
	CF	83:67	117:86	10.1	27/01/1998
	CHN	93:65	139:91	6.1	02/02/1998
	FG	69:81	84:96	7.6	06/01/1998
	HB	66:54	89:69	3.6	22/01/1998
	NUGN	36:38	43:47	14.2	17/01/1998
	OBI	100:81	136:103	6.6	31/01/1998
	OP	35:31	61:48	1.2	15/02/1998
	QBE	37:28	64:42	6.0	11/02/1998
	SMN	55:52	67:62	9.4	08/01/1998
	TI	43:47	67:69	6.0	06/02/1998
	TKS	47:53	57:62	9.2	06/01/1998
	VICN	48:52	58:62	4.4	10/01/1998
	WEKN	76:73	110:99	7.1	28/01/1998
	WEKS	73:77	101:99	15.5	26/01/1998
1998 Total		1033:988	1441:1282	$\bar{x}=7.2$	
Total		2394:2155	3358:2796		

total number of males caught over all colonies (Fig. 3a), or as the mean proportion of males among colonies (Fig. 3b). Based on the  $G$ -tests and the 95% binomial confidence intervals (Fig. 3a), the proportion of male pups significantly exceeded 0.5 in 1996 and 1997 only (1996:  $G_1=9.59$ ,  $P=0.002$ ; 1997:  $G_1=6.87$ ,  $P=0.009$ ; 1998:  $G_1=1.00$ ,  $P=0.317$ ; Fig. 3a).

Examining the proportion of male pups within each mass class revealed a significant increase from the light to heavy mass classes in all years studied (1996:  $G_1=36.14$ ,  $P<0.001$ , Fig. 4a; 1997:  $G_1=111.61$ ,  $P<0.001$ , Fig. 4b; 1998:  $G_1=100.84$ ,  $P<0.001$ , Fig. 4c), and for all years combined ( $G_1=111.61$ ,  $P<0.001$ , Fig. 4d). It should be noted that there is no evidence that birth dates in *A.*

*forsteri* in New Zealand are sex-biased (Schulman 1996), so the patterns observed in Fig. 4 are due to higher mass at all ages for male pups (Crawley 1975; Mattlin 1981; Bradshaw et al. 2003).

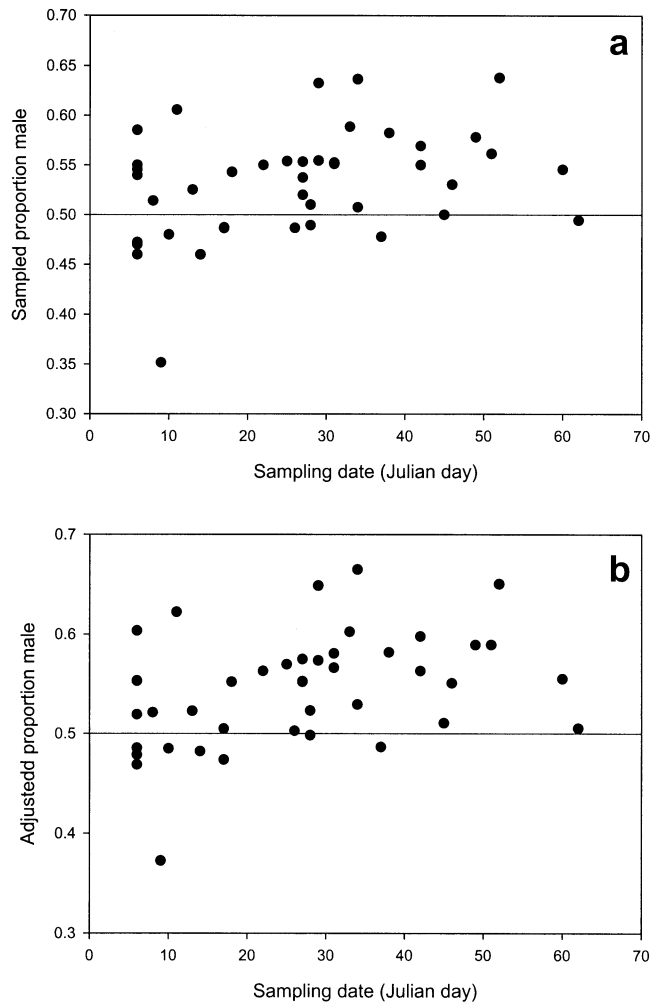
Using the data adjusted for differential capture probability, the proportion of males in each sample again exceeded 0.5 in all years, expressed both as total males caught over all colonies (Fig. 3c), or as the mean proportion among colonies (Fig. 3d). In fact, the adjustment for capture probability increased the proportion of males in all 3 years. The  $G$ -tests revealed that the adjusted ratios in all years were significantly male-biased (1996:  $G_1=21.66$ ,  $P<0.001$ ; 1997:  $G_1=27.39$ ,  $P<0.001$ ; 1998:



**Fig. 1** **a** Proportion of male pups per colony in the sample of pups captured relative to sample size ( $\log_{10}$  number of pups caught per colony) combining data from all 3 years (1996–1998). **b** Proportion of male pups per colony adjusted for mass-specific capture probabilities relative to sample size ( $\log_{10}$  number of pups caught per colony) combining data from all 3 years (1996–1998)

$G_1=9.29$ ,  $P=0.002$ ), and the general trend for decreasing male bias with year remained (Fig. 3c, d).

Model selection using AIC with the adjusted data identified a single best model to explain the variation in sex ratios among colonies and years. That model included the terms *colony* and *year* and had an AIC weight of 0.866 ( $\chi^2_{17}=46.12$ ,  $P<0.001$ ). The next best model with only the *colony* term had low support (AIC weight=0.123), so was not considered further. The model including the interaction between *colony* and *year* had no support according to AIC (AIC weight  $<0.001$ ). Therefore, we conclude that sex ratio varied significantly among colonies and years, but there was no support for an interaction between these terms. Post-hoc  $G$ -tests of independence demonstrated that the sex ratio in 1998 was significantly less male-biased than in 1996 ( $G_1=6.23$ ,  $P=0.013$ ), but there was little difference between 1996 and 1997 ( $G_1=1.62$ ,



**Fig. 2** **a** Proportion of male pups per colony in the sample of pups captured relative to date of capture (Julian day) combining data from all 3 years (1996–1998). **b** Proportion of male pups per colony adjusted for mass-specific capture probabilities relative to date of capture (Julian day) combining data from all 3 years (1996–1998)

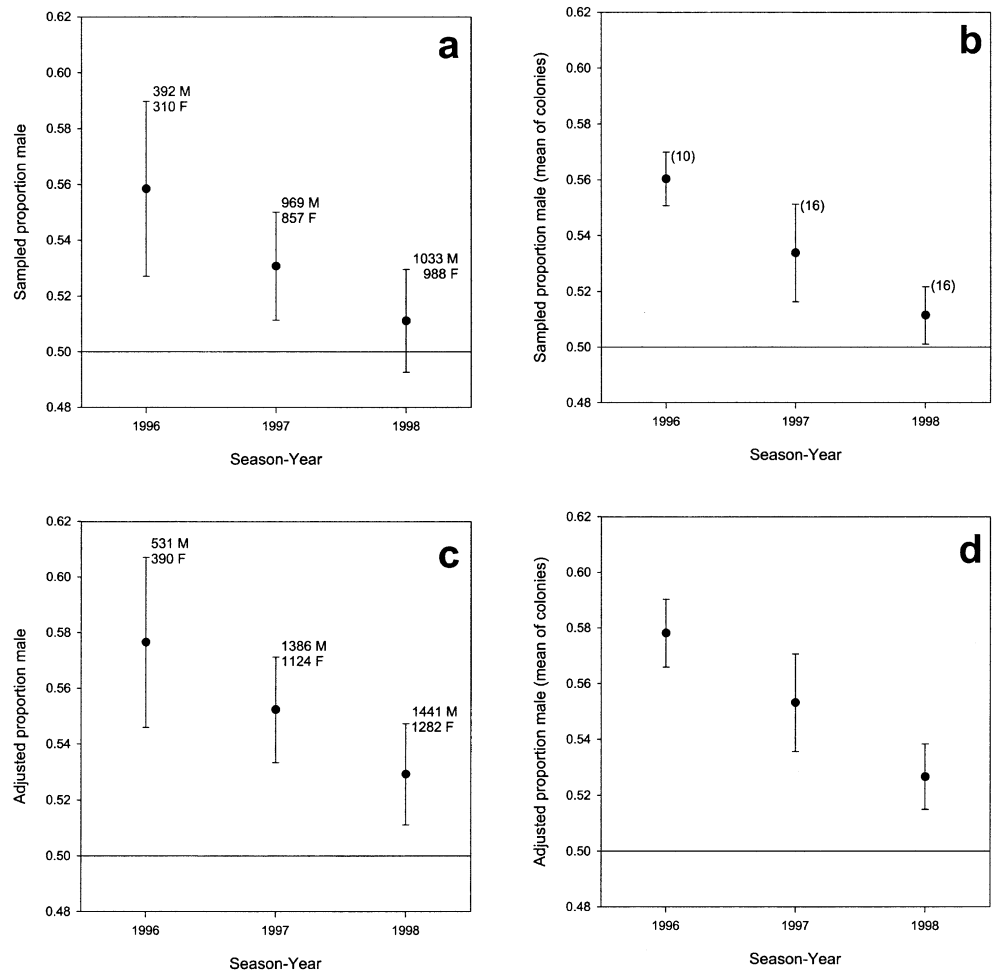
$P=0.203$ ), and a possible difference between 1997 and 1998 ( $G_1=2.78$ ,  $P=0.095$ ). Thus, we conclude that the less male-biased sex ratio in 1998 was mainly responsible for the significant *year* effect in the logistic regression model.

Pup densities (pups/100 m<sup>2</sup> colony area, Bradshaw et al. 2000a) are presented in Table 1. The analysis of sex ratio relative to pup density and mean body condition of pups per colony revealed no significant relationships. A randomised, linear regression of the proportion of male pups relative to colony density indicated no significant relationship for the sampled data ( $P_{20,000}=0.537$ , Fig. 5a) or the mass-adjusted data ( $P_{20,000}=0.595$ , Fig. 5b).

## Discussion

We found that sex ratios favoured males in all years, but the magnitude of this bias varied among years. This pattern was also consistent among colonies, as expressed

**Fig. 3** **a** Proportion of male pups per year in the sample of pups captured summed over all colonies (with 95% binomial confidence intervals). Sample sizes indicate the total number of male (*M*) and female (*F*) pups caught in the original samples. **b** Proportion of male pups expressed as the mean proportion among colonies (with standard errors). Sample sizes indicate the total number of colonies sampled per year (in parentheses). **c** Proportion of male pups adjusted for mass-specific capture probability and summed over all colonies. Sample sizes represent the estimated numbers of male and female pups that would have been captured if there was an equal probability of capturing pups among mass classes. **d** Proportion of male pups adjusted for differential capture probability and averaged over all colonies

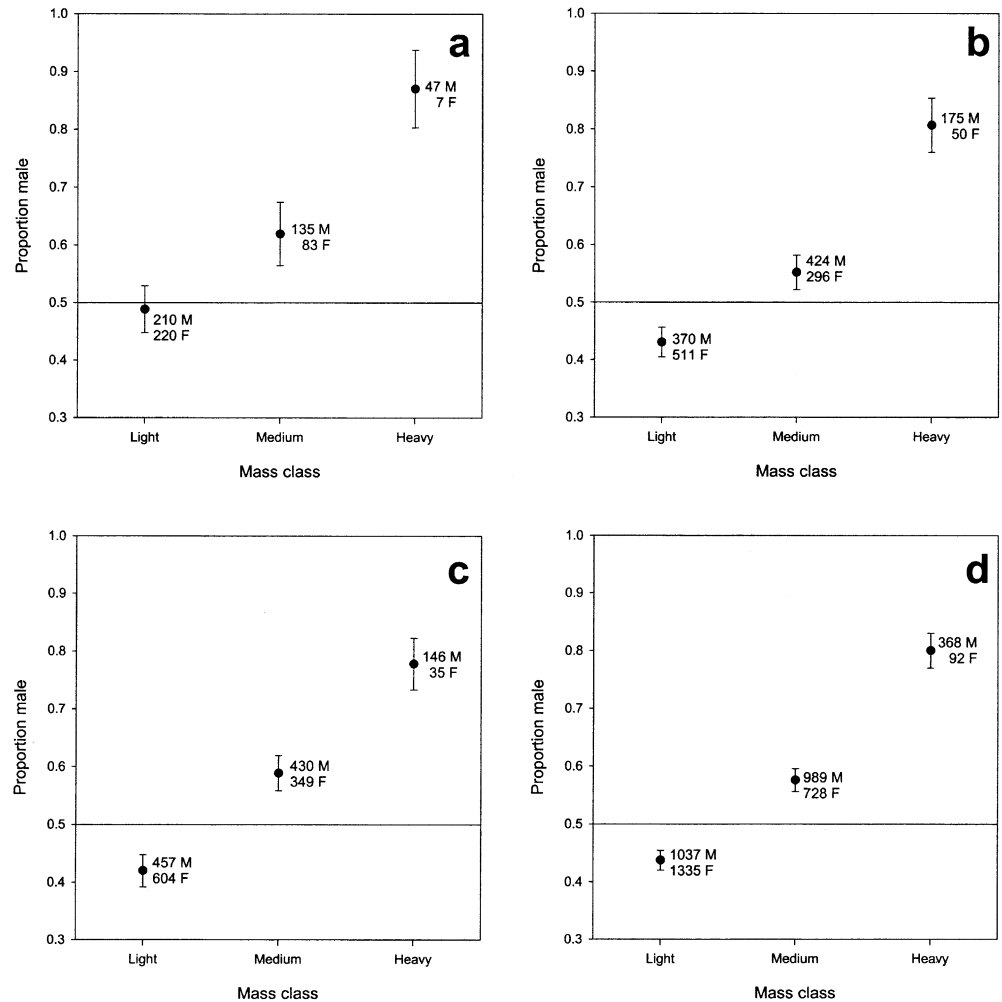


as the mean ratio over all colonies. The reduced male bias in the 1998 sex ratio relative to the previous years, both for the original and adjusted samples, may be related to the environmental conditions present during that year. Although we do not have direct measures of food availability prior to the pupping period, nor do we have data on mother condition during the study period, previous work has demonstrated a significant decline in pup condition in 1998 (Bradshaw et al. 2000a) during a strong El Niño event that year (Basher 1998). Further, Goldsworthy (1992) found that *A. forsteri* mothers in Australia were lighter immediately after a strong ENSO event (1989 La Niña) compared to the following year. Pup growth rates in the poor-resource year (1989) were similar for male and female pups; however, in 1990, the growth rate of male pups was significantly greater than that of females. In our study, only the 1998-unadjusted sex ratio was not significantly different from unity, and there was a lower proportion of males in 1998 relative to other years. This observation is consistent with the prediction that when resources are plentiful, more mothers produce male pups, or more male pups survive (Trillmich 1986). However, when the relative food availability declines as is postulated to occur during

ENSO years such as 1998, the bias may disappear or decline.

It has been shown in primate populations where the growth rate is low (and competition is high), that high-ranking females produced more daughters (van Schaik and Hrdy 2002). In contrast, ungulate mothers produced more sons under the TW hypothesis when density and thus, competition, was low (Kruuk et al. 1999). Such relationships led Cockburn et al. (2002) to suggest that while population density is low, the TW model operates because it is advantageous to transfer good condition to sons. However, when population density is high, the LRC hypothesis may be a more appropriate model to predict sex-ratio variation. Although some researchers have failed to find bias in otariid pup sex ratios (Bonner 1968; Stirling 1971; Boyd and McCann 1989; Goldsworthy and Shaughnessy 1994; Georges and Guinet 2001), we suggest that biases may only be detectable during years when resources are plentiful, when population density is low or, at least, when sample sizes are large (Rand 1956; Oosthuizen 1991; Shaughnessy 1993; West and Sheldon 2002). Indeed, because maternal expenditure in seal pups is assumed to be high for both sexes, it may be difficult to detect differences caused by environmental variation (Boltnev et al. 1998). It may also be difficult to detect

**Fig. 4** **a** The mass-specific (i.e. light, medium, heavy) proportion of male pups in the 1996 sample of pups captured summed over all colonies (with 95% binomial confidence intervals). Sample sizes indicate the total number of male (*M*) and female (*F*) pups caught in 1996. **b** Mass-specific proportion of male pups in the 1997 sample. **c** Mass-specific proportion of male pups in the 1998 sample. **d** Mass-specific proportion of male pups combining data from all 3 years (1996–1998)



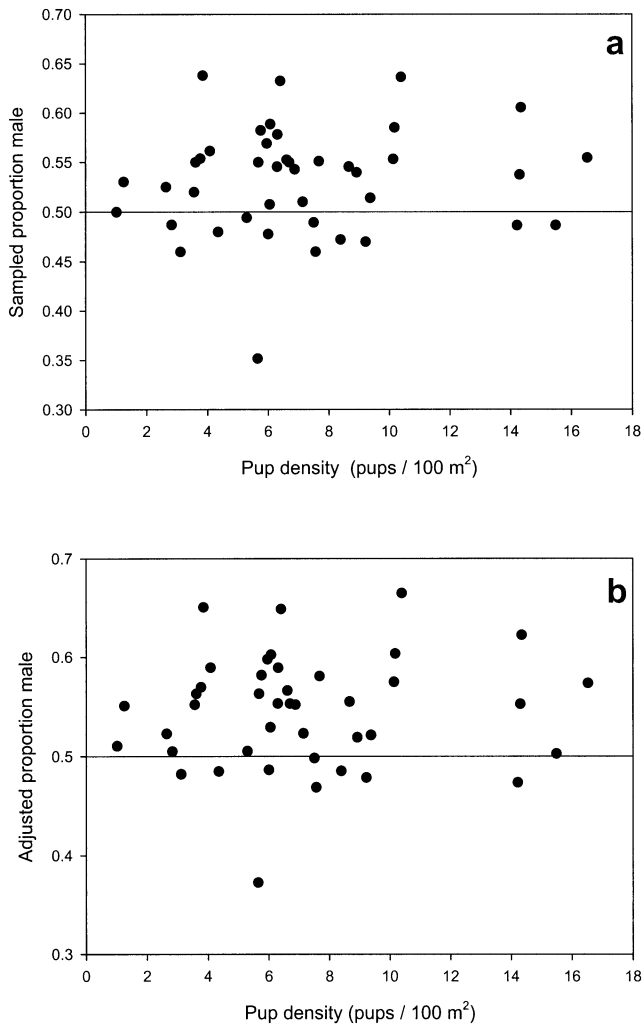
the effect of female condition on pup sex with small sample sizes. Further, the complex interactions of habitat heterogeneity (Bradshaw et al. 2000a, 2002), temporal variability in resource availability (Bradshaw et al. 2000a; Guinet et al. 2001; Lea et al. 2001), the varying effects of population density on relative resource availability (Cockburn et al. 2002), the degree of resource predictability (West and Sheldon 2002), and sex-biased dispersal capacity would necessarily result in a diverse array of sex ratios reported for otariid seals (Julliard 2000).

Several authors (Guinet et al. 2000; Arnould et al. 2001; Georges and Guinet 2001) suggest that post-parturition investment by fur-seal mothers does not vary with the sex of the pup; rather, it has been suggested that sons and daughters follow different growth strategies. It is therefore unlikely that differential post-partum pup mortality would be adaptive for female fur seals under most circumstances. As a monogamous species, a mother would lose an entire year of reproductive output, representing perhaps >10% of her lifetime reproductive output (Boyd et al. 1995). This suggests that only during periods of extreme food stress would it pay a mother to abandon her pup. Hence, it is far more likely that any sex ratio

modification, if adaptive in fur seals, should occur pre-partum (see Krackow 1995).

This, combined with the lack of a relationship between sex ratio and pup density, suggest that there has been selection for *A. forsteri* mothers in good condition to produce male pups. The rapid increase in pup production in many *A. forsteri* colonies during the study period (Lalas and Murphy 1998; Bradshaw et al. 2000b; Lalas and Bradshaw 2001) suggests that density was “low” in all years studied. The density-independent resource depletion hypothesised for 1998 is qualitatively different to the density-dependent resource depletion demonstrated by Kruuk et al. (1999). Further, the low densities observed may preclude the operation of the LRC model to explain adaptive sex-ratio bias in this species at this time. It is also more likely that selection for the sex bias observed occurs pre-partum. A number of mechanisms for the differential production of one sex have been proposed for mammals (Krackow 1995), such as gamete selection before conception (Trivers 1972; Simpson and Simpson 1982; James 1997), intra-uterine exposure to androgens (Clark and Galef Jr. 1995), or selective abortion or re-absorption of the foetus (Trivers and Willard 1973;





**Fig. 5** **a** Sampled proportion of males per colony relative to the mean density of pups (pups/100 m<sup>2</sup>) for all years combined. **b** Mass-adjusted proportion of males per colony relative to the mean density of pups for all years combined

Gosling 1986; Trites 1992; Arnbom et al. 1994; Guinet et al. 1998; Mison-Jooste 1999).

The maintenance of male-biased sex ratios in New Zealand fur seals, even during years of apparent resource depletion, suggests that a combination of theoretical models for adaptative sex ratios may apply to this species, as has been found for other mammals (e.g. primates, Packer et al. 2000). New Zealand fur seals, or more generally, fur seals, appear to meet many of the assumptions of the TW model. However, the TW model itself may not fully explain many of the aspects of maternal expenditure and investment because the relative reproductive costs of sons and daughters in otariids remain unclear (Costa et al. 1988; Trillmich 1996; Guinet et al. 2000; Arnould et al. 2001; Georges and Guinet 2001). In this study, the differential production of males when resources were plentiful, and the lack of density effects on sex ratios, appear to follow only some of the predictions of the TW model, and this may be enhanced by a degree

of temporal predictability in resource availability (West and Sheldon 2002). Indeed, New Zealand fur seals demonstrate little inter-annual variability in foraging behaviour (Harcourt et al. 2001), possibly due to their generalist diet and flexible foraging strategies (Harcourt et al. 2002). Further, male offspring in otariid species disperse more readily than females (Oosthuizen 1991; Boyd et al. 1998), so low-resource years may induce females in poorer-quality regions to switch to producing a son. We propose therefore that a trade-off in life-history strategies may be operating in this species. Low reproductive output (monotocous; one reproductive event per year) and high post-partum expenditure by mothers suggest there is a strong selection to maximise future reproductive benefit via pre-partum mechanisms of offspring sex determination and production. The apparent contradiction to the evolutionary stability of equal sex ratios (Fisher 1930) suggested by adaptive sex-ratio manipulation may be explained, in part, by the existence of negative temporal autocorrelation in sex ratios between years (Byholm et al. 2002). Although there was not enough temporal replication in our dataset to test this hypothesis, Byholm et al. (2002) suggested that a temporal lag results in local sex ratios that are corrected towards equality, as expected from frequency-dependent selection (Fisher 1930).

**Acknowledgements** Research was funded by the University of Otago. We also thank Allflex New Zealand (Palmerston North) for providing the plastic tags used to identify fur seal pups, Combined Rural Traders Society (Otago) for providing field equipment, and Next Stop Backpackers (Dunedin) for providing accommodation for volunteers. We particularly thank the Department of Zoology (University of Otago), New Zealand Department of Conservation, Landcare Research New Zealand, and New Zealand Sea Adventures (Kaikoura) for logistic support. We thank A. Anderson, G. Anderson, C. Bevers, K. Barton, C. Duncan, C. Littnan, N. McNally, I. Rasmussen, B. Thomas, M. Wright and the many volunteers who assisted with data collection. We thank R.J. Barker for providing statistical advice, and the editor, F. Trillmich, and two anonymous referees for greatly improving the manuscript. All animal treatment procedures were approved by the University of Otago Animal Ethics Committee (no. 83-95) and licensed under a New Zealand Department of Conservation Permit to Take Marine Mammals (30 July 1996).

## References

- Antonelis GA, Ragen TJ, Rooks NJ (1994) Male-biased secondary sex ratios of northern fur seals on the Pribilof Islands, Alaska, 1989 and 1992. In: Sinclair EH (ed) Fur seal investigations, 1992. Technical Memo NMFS-AFSC-45. US Department of Commerce, National Oceanographic and Atmospheric Administration, Seattle, pp 84–89
- Arnbom T, Fedak MA, Rothery P (1994) Offspring sex ratio in relation to female size in southern elephant seals, *Mirounga leonina*. Behav Ecol Sociobiol 35:373–378
- Arnould JPY, Boyd IL, Rawlins DR, Hindell MA (2001) Variation in maternal provisioning by lactating Antarctic fur seals (*Arctocephalus gazella*): response to experimental manipulation in pup demand. Behav Ecol Sociobiol 50:461–466
- Austad SN, Sunquist ME (1986) Sex-ratio manipulation in the common opossum. Nature 324:58–60

- Bartholomew GA (1970) A model for the evolution of pinniped polygyny. *Evolution* 24:546–559
- Basher RE (1998) The 1997/98 El Niño event: impacts, responses and outlook for New Zealand. 73. Ministry of Research, Science and Technology, Wellington
- Boltnev AI, York AE, Antonelis GA (1998) Northern fur seal young: interrelationships among birth size, growth, and survival. *Can J Zool* 76:843–854
- Bonner WN (1968) The fur seal of South Georgia. Rep. No. 56. British Antarctic Survey, London
- Boyd IL (2000) State-dependent fertility in pinnipeds: contrasting capital and income breeders. *Funct Ecol* 14:623–630
- Boyd IL, McCann TS (1989) Pre-natal investment in reproduction by female Antarctic fur seals. *Behav Ecol Sociobiol* 24:377–385
- Boyd IL, Lunn NJ, Rothery P, Croxall JP (1995) Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. *J Anim Ecol* 64:505–518
- Boyd IL, McCafferty DJ, Reid K, Taylor R, Walker TR (1998) Dispersal of male and female Antarctic fur seals (*Arctocephalus gazella*). *Can J Fish Aquat Sci* 55:845–852
- Bradshaw CJA, Lalas C, Perriman L, Harcourt RG, Best H, Davis LS (1999) Seasonal oscillation in shore attendance and transience of New Zealand fur seals. *Can J Zool* 77:814–823
- Bradshaw CJA, Davis LS, Lalas C, Harcourt RG (2000a) Geographic and temporal variation in the condition of pups of the New Zealand fur seal (*Arctocephalus forsteri*): evidence for density dependence and differences in the marine environment. *J Zool Lond* 252:41–51
- Bradshaw CJA, Lalas C, Thompson CM (2000b) Clustering of colonies in an expanding population of New Zealand fur seals (*Arctocephalus forsteri*). *J Zool Lond* 250:105–112
- Bradshaw CJA, Davis LS, Purvis M, Zhou Q, Benwell GL (2002) Using artificial neural networks to model the suitability of coastline for breeding by New Zealand fur seals. *Ecol Model* 148:111–131
- Bradshaw CJA, Barker RJ, Harcourt RG, Davis LS (2003) Estimating survival and capture probability of fur seal pups using multi-state mark-recapture models. *J Mammal* 84:65–80
- Buckland ST, Burnham KP, Augustin NH (1997) Model selection: an integral part of inference. *Biometrics* 53:603–618
- Buskirk SW, Lindstedt SL (1989) Sex biases in trapped samples of Mustelidae. *J Mammal* 70:88–97
- Byholm P, Ranta E, Kaitala V, Lindén H, Saurola P, Wikman M (2002) Resource availability and goshawk offspring sex ratio variation: a large-scale ecological phenomenon. *J Anim Ecol* 71:994–1001
- Calambokidis J, Gentry RL (1985) Mortality of northern fur seal pups in relation to growth and birth weights. *J Wildl Dis* 21:327–330
- Cameron EZ, Linklater WL (2000) Individual mares bias investment in sons and daughters in relation to their condition. *Anim Behav* 60:359–367
- Cameron EZ, Linklater WL, Stafford KJ, Veltman CJ (1999) Birth sex ratios relate to mare condition at conception in Kaimanawa horses. *Behav Ecol* 10:472–475
- Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton
- Clark AB (1978) Sex ratio and local resource competition in a prosimian primate. *Science* 201:163–165
- Clark MM, Galef BG Jr (1995) A gerbil dam's fetal intrauterine position affects the sex ratios of litters she gestates. *Physiol Behav* 57:297–299
- Clutton-Brock TH (1982) Parental investment in male and female offspring in mammals. In: Group KCS (ed) Current problems in sociobiology. Cambridge University Press, Cambridge, pp 223–247
- Clutton-Brock TH, Iason GR (1986) Sex ratio variation in mammals. *Rev Biol* 61:339–374
- Clutton-Brock TH, Albon SD, Guinness FE (1981) Parental investment in male and female offspring in polygynous mammals. *Nature* 289:487–489
- Clutton-Brock TH, Albon SD, Guinness FE (1984) Maternal dominance, breeding success and birth sex ratios in red deer. *Nature* 308:358–360
- Cockburn A, Legge S, Double MC (2002) Sex ratios in birds and mammals: can the hypotheses be disentangled? In: Hardy ICW (ed) Sex ratios: concepts and research methods. Cambridge University Press, Cambridge, pp 267–286
- Costa DP, Trillmich F, Croxall JP (1988) Intraspecific allometry of neonatal size in the Antarctic fur seal (*Arctocephalus galapagoensis*). *Behav Ecol Sociobiol* 22:361–364
- Côté SD, Festa-Bianchet M (2001) Offspring sex ratio in relation to maternal age and social rank in mountain goats (*Oreamnos americanus*). *Behav Ecol Sociobiol* 49:260–265
- Crawley MC (1975) Growth of New Zealand fur seal pups. *N Z J Mar Freshwater Res* 9:539–545
- Dickman CR (1988) Sex-ratio variation in response to interspecific competition. *Am Nat* 132:289–297
- Dittus WPJ (1998) Birth sex ratios in toque macaques and other mammals: integrating the effects of maternal condition and competition. *Behav Ecol Sociobiol* 44:149–160
- Doidge DW, Croxall JP, Baker JR (1984) Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. *J Zool Lond* 202:449–460
- Fisher RA (1930) The genetical theory of natural selection. Oxford University Press, Oxford
- Fowler CW (1990) Density dependence in northern fur seals (*Callorhinus ursinus*). *Mar Mammal Sci* 6:171–195
- Francis JM, Heath CB (1991) The effects of El Niño on the frequency and sex ratio of suckling yearlings in the California sea lion. In: Trillmich F, Ono KA (eds) Pinnipeds and El Niño: responses to environmental stress, vol 88. Springer, Berlin Heidelberg New York, pp 193–201
- Frank SA (1990) Sex allocation theory for birds and mammals. *Annu Rev Ecol Syst* 21:13–55
- Gehrt SD, Fritzell EK (1996) Sex-biased response of raccoons (*Procyon lotor*) to live traps. *Am Midl Nat* 135:23–32
- Gentry RL, Kooyman GL (1986) Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton
- Georges J-Y, Guinet C (2000a) Early mortality and perinatal growth in the subantarctic fur seal (*Arctocephalus tropicalis*) on Amsterdam Island. *J Zool Lond* 251:277–287
- Georges J-Y, Guinet C (2000b) Maternal care in the subantarctic fur seals on Amsterdam Island. *Ecology* 81:295–308
- Georges J-Y, Guinet C (2001) Prenatal investment in the subantarctic fur seal, *Arctocephalus tropicalis*. *Can J Zool* 79:601–609
- Goebel ME, Calambokidis J (1998) Neonatal growth and behavior. In: Gentry RL (ed) Behavior and ecology of the northern fur seal. Princeton University Press, Princeton, NJ, pp 233–242
- Goldsworthy SD (1992) Maternal care in three species of southern fur seal (*Arctocephalus* spp.). PhD Thesis, Monash University, Melbourne
- Goldsworthy SD, Shaughnessy PD (1994) Breeding biology and haul-out pattern of the New Zealand fur seal, *Arctocephalus forsteri*, at Cape Gantheaume, South Australia. *Wildl Res* 21:365–376
- Gosling LM (1986) Selective abortion of entire litters in the coypu: adaptive control of offspring production in relation to quality and sex. *Am Nat* 127:772–795
- Guinet C, Roux J-P, Bonnet M, Mison V (1998) Effect of body size, body mass, and body condition on reproduction of female South African fur seals (*Arctocephalus pusillus*) in Namibia. *Can J Zool* 76:1418–1424
- Guinet C, Lea M-A, Goldsworthy SD (2000) Mass change in Antarctic fur seal (*Arctocephalus gazella*) pups in relation to maternal characteristics at the Kerguelen Islands. *Can J Zool* 78:476–483
- Guinet C, Dubroca L, Lea MA, Goldsworthy S, Chereil Y, Duhamel G, Bonadonna F, Donnay J-P (2001) Spatial distribution of the foraging activity of Antarctic fur seal *Arctocephalus gazella* females in relation to oceanographic factors: a scale-dependent approach using geographic information systems. *Mar Ecol Prog Ser* 219:251–264
- Harcourt RG, Schulman AM, Davis LS, Trillmich F (1995) Summer foraging by lactating female New Zealand fur seals

- (*Arctocephalus forsteri*) off Otago Peninsula, New Zealand. *Can J Zool* 73:678–690
- Harcourt RG, Bradshaw CJA, Davis LS (2001) Summer foraging behaviour of a generalist predator, the New Zealand fur seal (*Arctocephalus forsteri*). *Wildl Res* 28:599–606
- Harcourt RG, Bradshaw CJA, Dickson K, Davis LS (2002) Foraging ecology of a generalist predator, the female New Zealand fur seal. *Mar Ecol Prog Ser* 227:11–24
- Hardy IC (1997) Possible factors influencing vertebrate sex ratios: an introductory overview. *Appl Anim Behav Sci* 51:217–241
- Hewison AJM, Andersen M, Gaillard J-M, Linnell JDC, Delorme D (1999) Contradictory findings in studies of sex ratio variation in roe deer (*Capreolus capreolus*). *Behav Ecol Sociobiol* 45:339–348
- James WH (1997) A potential mechanism for sex ratio variation in mammals. *J Theor Biol* 189:253–255
- Johnson CN, Ritchie EG (2002) Adaptive biases in offspring sex ratios established before birth in a marsupial, the common brushtail possum *Trichosurus vulpecula*. *Behav Ecol* 13:653–665
- Julliard R (2000) Sex-specific dispersal in spatially varying environments leads to habitat-dependent evolutionary stable offspring sex ratios. *Behav Ecol* 11:421–428
- Kojola I, Eloranta E (1989) Influences of maternal body weight, age, and parity on sex ratio in semidomesticated reindeer (*Rangifer t. tarandus*). *Evolution* 43:1331–1336
- Krackow S (1995) Potential mechanisms for sex ratio adjustment in mammals and birds. *Biol Rev* 70:225–241
- Krackow S (1997) Maternal investment, sex-differentiated prospects, and the sex ratio in wild house mice. *Behav Ecol Sociobiol* 41:435–443
- Kruuk LEB, Clutton-Brock TH, Albon SD, Pemberton JM, Guinness FE (1999) Population density affects sex ratio variation in red deer. *Nature* 399:459–461
- Lalas C, Bradshaw CJA (2001) Folklore and chimerical numbers: review of a millennium of interaction between fur seals and humans in the New Zealand region. *N Z J Mar Freshwater Res* 35:477–497
- Lalas C, Harcourt R (1995) Pup production of the New Zealand fur seal on Otago Peninsula, New Zealand. *J R Soc N Z* 25:81–88
- Lalas C, Murphy B (1998) Increase in the abundance of New Zealand fur seals at the Catlins, South Island, New Zealand. *Roy Soc N Z* 28:287–294
- Lea M-A, Hindell MA, Guinet C, Goldsworthy S (2001) Variability in the diving activity of Antarctic fur seals, *Arctocephalus gazella*, at Iles Kerguelen. *Polar Biol* 25:269–279
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118
- Lunn NJ, Arnould JPY (1997) Maternal investment in Antarctic fur seals: evidence for equality in the sexes. *Behav Ecol Sociobiol* 40:351–362
- Lunn NJ, Boyd IL (1991) Pupping-site fidelity of Antarctic fur seals at Bird Island, South Georgia. *J Mammal* 72:202–206
- Manly BFJ (1997) Randomization, bootstrap and Monte Carlo methods in biology. Chapman & Hall, London
- Mattlin RH (1981) Pup growth of the New Zealand fur seal *Arctocephalus forsteri* on the Open Bay Islands, New Zealand. *J Zool Lond* 193:305–314
- Mattlin RH (1987) New Zealand fur seal, *Arctocephalus forsteri*, within the New Zealand region. In: Croxall JP, Gentry RL (eds) Status, biology, and ecology of fur seals. National Marine Fisheries Service, Cambridge, pp 49–51
- Maynard-Smith J (1980) A new theory of sexual selection. *Behav Ecol Sociobiol* 7:247–251
- Mison-Jooste V (1999) Contribution à l'étude de la biologie des populations de l'otarie à fourrure du Cap (*Arctocephalus pusillus pusillus*): les soins maternels diffèrent-ils en fonction du sexe du jeune? PhD Thesis, University of Lyons
- Nichols JD, Sauer JR, Pollock KH, Hestbeck JB (1992) Estimating transition probabilities for stage-based population projection matrices using capture-recapture data. *Ecology* 73:306–312
- Ono KA, Boness DJ (1991) The influence of El Niño on mother-pup behaviour, pup ontogeny, and sex ratios in the California sea lion. In: Trillmich F, Ono KA (eds) Pinnipeds and El Niño: responses to environmental stress, vol 88. Springer, Berlin Heidelberg New York, pp 185–192
- Ono KA, Boness DJ (1996) Sexual dimorphism in sea lion pups: differential maternal investment, or sex-specific differences in energy allocation? *Behav Ecol Sociobiol* 38:31–41
- Oosthuizen WH (1991) General movements of South African (Cape) fur seals *Arctocephalus pusillus pusillus* from analysis of recoveries of tagged animals. *S Afr J Mar Sci* 11:21–29
- Packer C, Collines DA, Eberley LE (2000) Problems with primate sex ratios. *Philos Trans R Soc Lond B* 355:1627–1635
- Palmer AR (2000) Quasireplication and the contract of error: lessons from sex ratios, heritabilities and fluctuating asymmetry. *Annu Rev Ecol Syst* 31:441–480
- Rand RW (1956) The Cape fur seal *Arctocephalus pusillus* (Schreber). Its general characteristics and moult. Investigational Report 21. Division of Fisheries South Africa, Cape Town
- Rutberg AT (1986) Lactation and fetal sex ratios in American bison. *Am Nat* 127:89–94
- Schaik CP van, Hrdy SB (2002) Intensity of local resource competition shapes the relationship between maternal rank and sex ratios at birth in cercopithecine primates. *Am Nat* 138:1555–1562
- Schulman AM (1996) Individual variation in maternal care and its effects on pup growth rate in the New Zealand fur seal (*Arctocephalus forsteri*) on the Otago Peninsula, New Zealand. MSc Thesis, University of Otago, Dunedin
- Shaughnessy PD (1993) Population estimates of the Cape fur seal *Arctocephalus pusillus*. 2. From tagging and recapturing. In: Boonstra HGvD (ed) Investigational Report 134. Sea Fisheries Research Unit, Cape Town
- Silk JB (1983) Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. *Am Nat* 121:56–66
- Simpson MJA, Simpson AE (1982) Birth sex ratios and social rank in rhesus monkey mothers. *Nature* 300:440–441
- Sokal RR, Rohlf FJ (1981) Biometry. The principles and practice of statistics in biological research, 2nd edn. Freeman, New York
- Stirling I (1971) Studies on the behaviour of the South Australian fur seal, *Arctocephalus forsteri* (Lesson). II. Adult females and pups. *Aust J Zool* 19:267–273
- Trillmich F (1986) Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. *Behav Ecol Sociobiol* 19:157–164
- Trillmich F (1996) Parental investment in pinnipeds. *Adv Stud Behav* 25:533–577
- Trillmich F, Kooyman GL (2001) Field metabolic rate of lactating female Galapagos fur seals (*Arctocephalus galapagoensis*): the influence of offspring age and environment. *Comp Biochem Physiol A* 129:741–749
- Trites AW (1991) Fetal growth of northern fur seals: life-history strategy and sources of variation. *Can J Zool* 69:2608–2617
- Trites AW (1992) Fetal growth and the condition of pregnant northern fur seals off western North America from 1958 to 1972. *Can J Zool* 70:2125–2131
- Trites AW (1993) Biased estimates of fur seal pup mass: origins and implications. *J Zool Lond* 229:515–525
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man 1871–1971. Aldine, Chicago, pp 136–179
- Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90–92
- West SA, Sheldon BC (2002) Constraints in the evolution of sex ratio adjustment. *Science* 295:1685–1688
- Williams GC (1979) The question of adaptive sex ratio in outcrossed vertebrates. *Proc R Soc Lond B* 205:567–580