Jong-yoon Kim · Robbin W. Thorp

Maternal investment and size-number trade-off in a bee, *Megachile apicalis,* in seasonal environments

Abstract Maternal investment in offspring size and number differed between spring- and summer-emerging individual females of *Megachile apicalis*, a solitary multivoltine bee. Data from experimentally initiated female populations indicated that spring-emerging females produced a relatively large number of progeny but allocated a small amount of food to each, resulting in small progeny. Adult females of larger body sizes provisioned food at a greater rate than did smaller females, and this body-size effect was significant in spring-emerging females. The large body size of these females allowed them to increase the number of progeny produced under the abundant floral resources that occurred during the spring. Conversely, summer-emerging females produced fewer progeny under the diminishing resources for brood production, but allocated each with more food, producing larger progeny, most of which emerged in the spring of the following year. Field data using trap-nests also indicated the same pattern of seasonal offspring size allocation found in the experimental populations. This maternal investment strategy entails a trade-off between the size and number of progeny, so that the daughters upon emergence can best perform in their brood production under the seasonally variable environments where they reproduce.

Keywords Maternal investment · *Megachile apicalis* · Leaf-cutter bee · Brood production · Offspring size

J.-y. Kim (✉)
Laboratory of Biomicromachine,
Department of Farm Mechanization,
National Agriculture Research Center, 3-1-1 Kannondai, Tsukuba,
305-8666 Japan
e-mail: jkim@affrc.go.jp
Fax: +81-298-387171

J.-y. Kim · R.W. Thorp
Department of Entomology, University of California, Davis,
CA 95616, USA

Introduction

Parental investment varies seasonally in a wide group of animals (Vila and Cassini 1994; Braby and Jones 1995; Mauck and Grubb 1995; Rytkonen 1995). This variation is often engendered by adaptive investment strategies to optimize their reproductive success. One of the strategies involves the determination of offspring size, whose seasonal variation is reported in diverse taxa (Nussbaum 1981; Brody and Lawlor 1984; Wiklund and Karlsson 1984; McGinley et al. 1987; Perrin 1988; Landa 1992; Sinervo et al. 1992; Mangel et al. 1994). A common phenomenon shown in these studies is that there are predictable patterns of seasonal fluctuations in offspring size. Discussions have often centered on the question of whether these seasonal fluctuations are produced by biotic or abiotic conditions (Brody and Lawlor 1984; Perrin 1988). However, little has been done to determine if these fluctuations are adaptive, and if so, what selective pressures favor such plasticity (Landa 1992).

Size variation is common in solitary wasps and bees, in which it is largely determined by the amount of food that a single reproductive female allocates for her individual progeny (Trivers and Willard 1973; Trivers and Hare 1976; Cowan 1981; Freeman 1981a, 1981b; Sugiura and Maeta 1989; Johnson 1990; Danforth 1990). Numerous studies indicate that a female adjusts her food allocation to progeny according to some seasonally variable ecological factors such as availability of floral resources (Torchio and Tepedino 1980; Tepedino and Torchio 1982; Frohlich and Tepedino 1986; Sihag 1986; Minckley et al. 1994), low temperatures for overwintering progeny (Tepedino and Torchio 1982; Tepedino and Parker 1988), local mate competition (Freeman 1981b) and nest parasitism (Visscher and Danforth 1993).

In this study, we examine the progeny size and number allocation in a solitary leaf-cutter bee, *Megachile apicalis* Spinola, by contrasting the different strategies between spring-emerging and summer-emerging females. The questions addressed are:

1. How differently do spring- and summer-emerging individual female bees allocate size and number of progeny under different availability of resources?
2. What are the factors that select for the allocation strategy of each group of females?

To answer these questions, We reared populations of *M. apicalis* in outdoor nest sites and measured progeny allocation in each individual female. Results of the measurements are discussed in the light of a trade-off between progeny size and number allocation.

Materials and methods

The insect

Megachile apicalis Spinola is a leaf-cutter bee accidentally introduced into the western United States from Europe. It was first collected in southern California in 1981 and is presently found throughout northern California to southern Oregon and eastern Washington (Cooper 1984; Stephen 1987; Thorp et al. 1992; Barthell and Thorp 1995). It is expanding its habitats and has a higher reproductive rate than native *Megachile* species in California (Thorp et al. 1992). Like most other *Megachile*, females of this species construct linear nests of leaf-covered brood cells ("cells" hereafter) in natural cavities like tree holes and hollow twigs. Each individual female lines the interior of these cavities with leaf materials to form a cell, provisions it with pollen and nectar, lays an egg and completes the cell by capping it with leaf materials. She repeats this cell production process until reaching the cavity entrance which she later seals with additional leaf materials. Because *M. apicalis* females readily use artificial nest cavities and tend to have gregarious nesting habits, large numbers of them can be reared in the field by providing domiciles, artificial nest blocks with drilled holes. *M. apicalis* populations in central California have at least three generations per year. The first generation, which has overwintered and emerged in the spring, is categorized as "spring generation", and both the second and third generations emerging in the summer are together categorized as "summer generation". Thus, hereafter, females of these two categories are called "spring females" and "summer females", respectively. Most of the summer females produce overwintering broods that emerge as a spring generation of the following year.

Experimental procedure

We collected about 2000 overwintering cocoons of *M. apicalis* from artificial nests (described later) at the University of California (UC) at Davis, Bee Biology Facility in the fall of 1993. To initiate an experimental population, we used the emerging first generation and studied the nesting activity of females at a field site of 3500 m² near the Bee Biology Facility during 1994. The site was an abandoned field covered with weeds dominated by patches of yellow star-thistle (*Centaurea solstitialis* L.), which provided pollen and nectar resources for foraging females. We monitored flowering phenology of the yellow star thistle by counting open flowers at ten randomly-selected permanent plots of 1 m² from early June to early October.

To provide nest sites for female bees, we made a domicile of artificial nest cavities of 11 bundles of nine wood sticks (15×2.5×2.5 cm) each. In each stick, a tunnel was drilled to a depth of 13 cm, and a paper straw (Sweet Heart; 1/4 inch diameter) was inserted into it. The domicile was installed 200 m west of the yellow star-thistle field and 1.5 m above ground. To distinguish between bees of spring and summer generations, we marked emerging bees on the median cell of their forewings with a different color of Sharpie ink for each generation and released them at the domicile. Females that started a nest were temporarily removed from their nests at night, kept cool in a vial placed in an ice bath to arrest their movement, and weighed. We then marked them again with dots of colored paints on their thoraces before returning them to the nests. We observed the nests daily by removing the paper straws from the domicile and recorded for each individual female the number of cells completed or in the process of provisioning.

We collected nest data for females that produced either summer-emerging or spring-emerging progeny, and most females observed were in this category. There were a few females that produced mixed broods of the two groups of progeny, and these broods were excluded from the data analyses. These were five spring females that produced a few overwintering progeny (6–18) between late July and early August, and four summer females that produced a few emerging third generation progeny (10–13) after early August.

To measure fresh cell weights, we harvested completed cells within 2 days after being capped and reared them in an incubator (25–30°C, 70–90% relative humidity). Emerging adults were sexed and weighed (wet weight). Among these adults, we released only females at the domicile to minimize sib-mating. Overwintering bees were kept outdoors in a tightly sealed container to avoid infestations from parasitic wasps (e.g., *Mellitobia* sp.).

We measured fecundity as the total number of cells produced by individual females, and longevity as the total time in days that individual females nested in the domicile. We calculated for each female the rate of cell production (cells/day) dividing the fecundity by longevity, and the rate of cell provisioning by dividing the total weight of entire cells produced by the longevity (cell weight/day). To monitor a gradual seasonal change in cell provisioning rate, we obtained a function of cell provisioning rate over time (cell weight/day) for all females observed. We did this by calculating a cell provisioning rate for each completed nest, to which we assigned a date of production in the middle of the series of cells in the nest.

Additional data from experimentally initiated populations were included in the analysis. These data were collected from the first completed nests of 40 summer females in 1993 and all nests of six spring females in 1995.

To monitor seasonal patterns of change in progeny size, one must analyze field data at more than one locality for more than one season because progeny size may be influenced by changing ecological factors such as resource heterogeneity between years and localities (Frohlich and Tepedino 1986). We collected nest data (1989–1991) of *M. apicalis* at the San Luis National Wildlife Refuge (SLNWR). These data were extracted from the long-term ecological monitoring research on cavity-nesting solitary bees in California conducted from 1988 to 1995 (see Thorp et al. 1992; and Frankie et al. 1998). The refuge lies within the historic flood plain of the San Joaquin river and consists of 6200 ha of grasslands, wetlands and riparian habitat.

To systematically monitor nesting bee population, we employed a trap-nesting technique (see Krombein 1967) using block sampling units (BSUs).

Each BSU contained several straight-grained pine sticks [stick sampling unit (SSU): each measuring 19×23×117 mm, with a tunnel drilled lengthwise to a depth of 10 cm]. They were arranged in a standard design within the block (see Thorp et al. 1992). Each BSU used in 1990 contained a total of 12 SSU, which were divided equally into three tunnel sizes: 4.7, 6.3 and 7.8 mm in diameter. BSUs used in 1989 had a different design: two of 4.7-mm-, two of 6.3-mm-, four of 7.8-mm-, two of 9.4-mm-, and two of 11.0-mm-diameter tunnels. The depths of tunnels varied as follows: 4.7-<6.3-<7.8-<9.4- and 11.0-mm-diameter tunnels. To minimize the influence of this difference in BSU design, only nests from SSUs of diameters 4.7, 6.3 and 7.8 mm were analyzed. We hung each BSU on a nail 1.5–2 m above ground on mostly vertical trunks or branches of live trees and replaced the BSU every 3 weeks at each site (15 sites in 1989 and nine sites in 1990). When bringing collected BSUs to the laboratory, we affixed a small glass vial with masking tape over the nest entrance of each harvested stick with at

least one completed *M. apicalis* cell. We reared the stick contents at room temperatures (18–22 C) and collected the emerging adult progeny in the glass vials. We measured the head width of these adult progeny to the nearest 0.01 mm using an ocular micrometer. If no adult bees emerged by early November, we allowed them to overwinter in a cold room (10 C) and to emerge at room temperatures in the following May and June. Voucher specimens of all bees are deposited in the R. M. Bohart Museum of Entomology, UC Davis.

Results

Seasonal activity patterns

Nesting activity at the domicile extended from early June to early October, during which three generations of females nested in 1994 [spring females, *n*=43; summer females, *n*=59 (second generation, *n*=52; third generation, *n*=7); Fig. 1A]. More than half of the spring females (28

out of 43) completed their second nest at the domicile, while <30% (13 out of 59) of the summer females did so, with the rest leaving the domicile. This was presumably due to the dearth of flowers after mid-August. Floral abundance started at a low level and rapidly increased until it reached a peak around mid-July, after which it gradually declined (Fig. 1A).

Seasonal changes in the sizes of females and their progeny

Body size significantly differed between spring and summer females (Table 1). The mean weight of the spring females was 19% larger than that of the summer females. There was a change in the weight of cells produced over the season, from lighter to heavier cells (Fig. 1B). As a result, progeny produced by summer females were significantly heavier than those produced by spring females (Table 1). A similar pattern was also found for trap-nest data from SLNWR (Fig. 2A).

Seasonal changes in cell production rate

Females' cell production and provisioning rates also changed over the season. Spring females produced and provisioned cells at a higher rate than summer females (Table 1). The cell provisioning rate was positively correlated with female body size for spring females but not for summer females (Fig. 2B). On a finer scale, the change in cell provisioning rate was characterized by a decline over the season (Fig. 1C).

Fecundity and longevity

Data from the domicile indicated that spring females had significantly higher fecundity than summer females
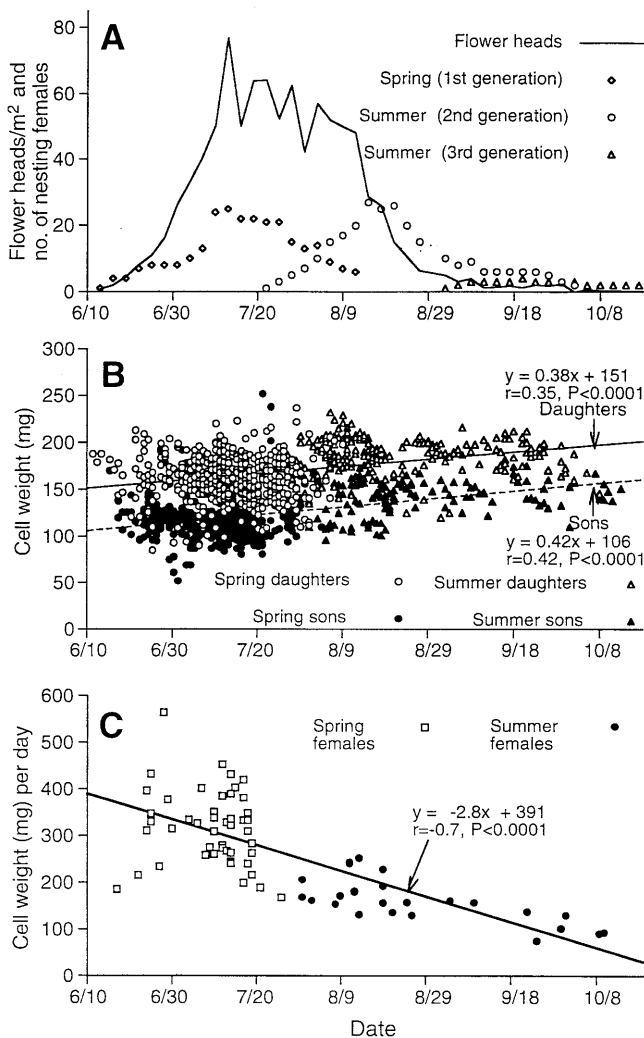

Fig. 1 Seasonal trends of **A** flower phenology and number of nesting females, **B** cell weights, and **C** cell provisioning rate of spring and summer females at Davis in 1994

Table 1 Comparison between spring and summer females and their progeny in wet adult body weights and cell production rates, fecundity (total number of cells produced) and longevity (total number of days taken to produce these cells) at Davis in 1994. Results reflect *t*-values from unpaired *t*-tests

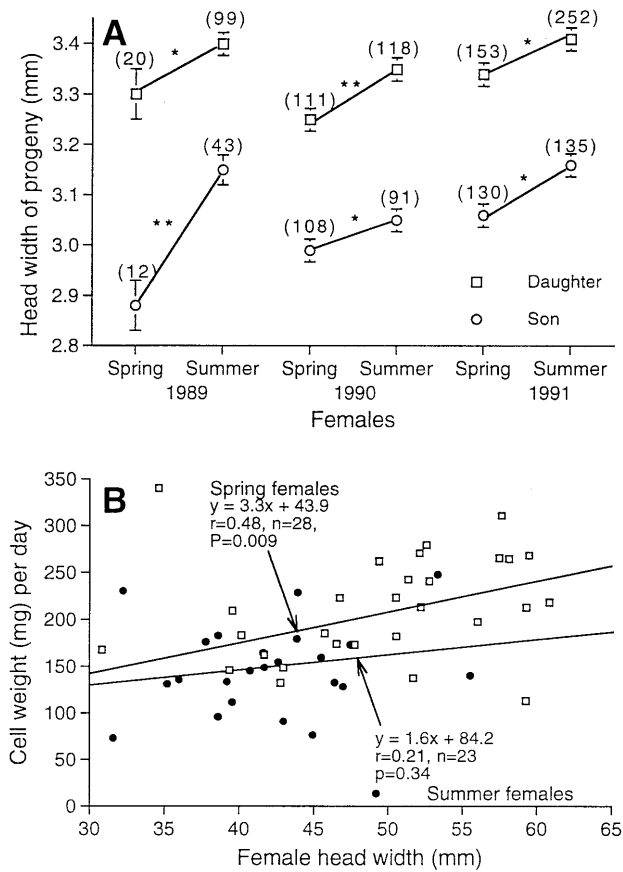| Bees	Spring females		Summer females		*t*	*P*
	n	Mean±SE	*n*	Mean±SE		
Wet adult body weight						
Females	28	49.8±1.4	23	41.9±1.2	4.1	<0.0001
Daughters	379	43.7±0.4	168	45.8±0.4	3.2	0.017
Sons	333	27.6±0.3	111	30.6±0.4	4.2	<0.0001
Cell production						
No. cell/day	28	1.5±0.1	23	0.9±0.1	6.5	<0.0001
Cell weight (mg)/day	28	207±10	23	152±10	4.0	0.0002
Fecundity	28	37.2±2.3	23	15.7±1.1	7.9	<0.0001
Longevity	28	25.2±1.4	23	19.0±1.6	3.0	0.046

Fig. 2A,B Comparison between spring and summer females. **A** Mean head widths (±SE) of their progeny during 3 continuous years from 1989 to 1991 at San Luis National Wildlife Refuge. Differences between the two groups of females were significant at **$P<0.0001$; *$P<0.05$ according to unpaired *t*-test. *Numbers above the bars* indicate the number of progeny sampled. **B** Cell production rate as a function of female head width of spring and summer females at Davis in 1994

(Table 1). This difference is partially attributable to the greater tendency of the summer females to disappear from the domicile than spring females. However, the slow cell production by the summer females was likely to keep their fecundity at a much lower level than that of the spring females. The spring females had slightly higher longevity than summer females (Table 1).

Discussion

This study demonstrated that the females of *M. apicalis* switched from producing a larger number of smaller progeny early in the season when floral resources are abundant, to a smaller number of larger progeny later in the season when floral resources are scarce. We interpret this seasonal investment pattern as partly due to the positive correlation between female size and cell provisioning rates in spring, when floral resources are abundant, but not in summer. Since summer females produce

spring progeny, they benefit from producing larger females.

In nest-building solitary Hymenoptera, a reproductive female provides a number of resources: food, nests and egg yolk to increase the fitness of progeny. Costs of acquiring these resources vary in seasonally changing environments and influence cell provisioning rates in solitary bee species (Parker and Frohlich 1985; Minckley et al. 1994). In fact, a controlled experiment using caged *M. apicalis* demonstrated that the females increased the rate of cell provisioning by 1.3 times when the floral resource level was artificially doubled (Kim 1999).

The cell provisioning rate is one of the fitness measures that are positively correlated with female size in *M. apicalis* (Kim 1997). This correlation was intensified for spring females that foraged when the floral resources were abundant. The caged-bee experiment also demonstrated that larger females provisioned cells at a greater rate than smaller females, particularly under a high floral resource level treatment (Kim 1996).

Currently, the mechanism as to how body size influences cell provisioning rate is unknown, but it is suggested that a larger body size gives flying bees better heat management in the relatively low air temperatures (Willmer 1986; Shmida and Dukas 1990). Since flight activity is an integral part of male mating behavior, body size pertaining to heat management may affect male mating success, although this needs to be tested. This may explain the result that the spring-emerging males had larger body sizes than summer-emerging males.

There are other life history traits known to be correlated to female size. For example, egg production often increases with female size. The increased cell production rate that necessitates greater egg production in the spring suggests that larger females may be less vulnerable to egg limitation (Mangel et al. 1994; Rosenheim et al. 1996). Cold hardiness is also known to be influenced by body size in bees, where larger individuals may overwinter more successfully (Tepedino and Parker 1986).

We attempt to explain this seasonal cycle of changing progeny by a trade-off between offspring size and number (Godfray et al. 1991; Lessells 1991; Roff 1992; Stearns 1992). Dividing resources into smaller amounts for each progeny allows them to increase the potential of increasing the total number of progeny produced. Such allocation is beneficial to spring females, who had a higher cell production rate than summer females. Therefore, the large spring females can have a head start early in the nesting season by quickly producing a large number of small summer progeny by using the large amount of floral resources available.

For a summer female, being smaller may be beneficial when nest-site availability declines. *M. apicalis* females are known to modify internal dimensions of natural cavities by adjusting the number of leaf linings, and smaller females have a wider range of nest-site availability than larger females that can nest only in natural cavities of larger internal diameters (Kim 1992; Thorp et al.

1992; Frankie et al. 1998). However, being smaller becomes more disadvantageous when competition for nest sites increases. The competition becomes intensified when the nest-site availability decreases due to more occupied nests by overwintering broods of cavity nesters (Krombein 1967; Danks 1971), or when local population densities of conspecifics increases, and larger females usurp nests from smaller females (Barthell and Thorp 1995), although the experimental population in this current research did not give rise to such high densities.

References

Barthell JF, Thorp RW (1995) Nest usurpation among females of an introduced leaf-cutter bee, *Megachile apicalis*. Southwest Entomol 20:117–124

Braby MF, Jones RE (1995) Reproductive patterns and resource allocation in tropical butterflies: Influence of adult diet and seasonal phenotype on fecundity, longevity and egg size. Oikos 72:189–204

Brody MS, Lawlor LR (1984) Adaptive variation in offspring size in the terrestrial isopod, *Armadillidium vulgare*. Oecologia 61:55–59

Cooper KW (1984) Discovery of the first resident population of the European bee, *Megachile apicalis*, in the United States (Hymenoptera: Megachilidae). Entomol News 95:225–229

Cowan DP (1981) Parental investment in two solitary wasps *Ancistrocerus adiabatus* and *Euodynerus foraminatus* (Eumenidae: Hymenoptera). Behav Ecol Sociobiol 9:95–102

Danforth BN (1990) Provisioning behavior and the estimation of investment ratios in a solitary bee, *Calliopsis (Hypomacrotera) persimilis* (Cockerell) (Hymenoptera: Andrenidae). Behav Ecol Sociobiol 27:159–168

Danks HV (1971) Populations and nesting-sites of some aculeate Hymenoptera nesting in *Rubus*. J Anim Ecol 40:63–77

Frankie GW, Thorp RW, Newstrom LE, Rizzardi MA, Barthell JF, Griswold TL, Kim J-Y, Kappagoda S (1998) Monitoring solitary bees in modified wildland habitats: implications for bee ecology and conservation. Environ Entomol 27:1137–1148

Freeman BE (1981a) Parental investment and its ecological consequences on the solitary wasp *Sceliphron assimile* (Dahlbom) (Sphecidae). Behav Ecol Sociobiol 9:261–268

Freeman BE (1981b) Parental investment, maternal size and population dynamics of a solitary wasp. Am Nat 117:357–362

Frohlich DR, Tepedino VJ (1986) Sex ratio, parental investment, and interparent variability in nesting success in a solitary bee. Evolution 40:142–151

Godfray HCJ, Partridge L, Harvey PH (1991) Clutch size. Annu Rev Ecol Syst 22:409–429

Johnson MD (1990) Female size and fecundity in the small carpenter bee, *Ceratina calcarata* (Robertson) (Hymenoptera: Anthophoridae). J Kans Entomol Soc 63:414–419

Kim J-Y (1992) Nest dimensions of two leaf-cutter bees (Hymenoptera: Megachilidae). Ann Entomol Soc Am 85:85-90

Kim J-Y (1996) Maternal investment and reproductive strategies of an adventive leaf-cutter bee, *Megachile apicalis* (Hymenoptera: Megachilidae). PhD thesis. University of California, Davis, Calif.

Kim J-Y (1997) Female size and fitness in the leaf-cutter bee *Megachile apicalis*. Ecol Entomol 22:275–282

Kim J-Y (1999) Influence of resource level on maternal investment in a leaf-cutter bee (Hymenoptera: Megachilidae). Behav Ecol 10:552–556

Krombein KV (1967) Trap-nesting wasps and bees. Life histories, nests and associates. Smithsonian Institution Press, Washington D.C.

Landa K (1992) Adaptive seasonal variation in grasshopper offspring size. Evolution 46:1553–1558

Lessells CM (1991) The evolution of life histories. In: Krebs JR, Davies NB (eds) Behavioural ecology. Blackwell, Oxford, pp 32–68

Mangel M, Rosenheim JA, Adler FR (1994) Clutch size, offspring performance and intergenerational fitness. Behav Ecol 5:412–417

Mauck RA, Grubb TC Jr (1995) Petrel parents shunt all experimentally increased reproductive costs to their offspring. Anim Behav 49:999–1008

McGinley MA, Temme DH, Geber MA (1987) Parental investment in offspring in variable environments: theoretical and empirical considerations. Am Nat 130:370–398

Minckley RL, Wcislo WT, Yanega D (1994) Behavior and phenology of a specialist bee (*Dieunomia*) and sunflower (*Helianthus*) pollen availability. Ecology 75:1406–1419

Nussbaum RA (1981) Seasonal shifts in clutch size and egg size in the side-blotched lizard, *Uta stansburiana* Baird and Girard. Oecologia 49:8–13

Parker FD, Frohlich DR (1985) Studies on management of the sunflower leafcutter bee *Eumegachile pugnata* (Say) (Hymenoptera: Megachilidae). J Apicult Res 24:125–131

Perrin N (1988) Why are offspring born larger when it is colder? Phenotypic plasticity for offspring size in the cladoceran *Simocephalus vetulus* (Müller). Funct Ecol 2:283–288

Roff DA (1992) The evolution of life histories: theory and analysis. Chapman and Hall, New York

Rosenheim JA, Nonacs P, Mangel M (1996) Sex ratios and multifaceted parental investment. Am Nat 148:501–535

Rytkonen S (1995) Parental care in the willow tit (*Parus montanus*): Nest defense and nestling provisioning in the light of the parental investment theory. Acta Univ Oulu Ser A Sci Rerum Nat 265:1–37

Shmida A, Dukas R (1990) Progressive reduction in the mean body sizes of solitary bees active during the flowering season and its correlation with the sizes of bee flowers of the mint family (Lamiaceae). Isr J Bot 39:133–141

Sihag RC (1986) Reproduction in alfalfa pollinating sub-tropical megachilid bees. 5. Effect of different feeding conditions on the ovarian recrudescence and haemolymph protein synthesis. Zool Anz 217:89–102

Sinervo B, Doughty P, Huey RB, Zamudio K (1992) Allometric engineering: a causal analysis of natural selection on offspring size. Science 258:1927–1930

Stearns S (1992) The evolution of life histories. Oxford University Press, Oxford

Stephen WP (1987) *Megachile (Eutricharaea) apicalis*, an introduced bee with potential as a domesticable alfalfa pollinator. J Kans Entomol Soc 60:583–584

Sugiura N, Maeta Y (1989) Parental investment and offspring sex ratio in a solitary Mason bee, *Osmia cornifrons* (Radoszkowski) (Hymenoptera, Megachilidae). Jpn J Entomol 57:861–875

Tepedino VJ, Parker FD (1986) Effect of rearing temperature on mortality, second-generation emergence, and size of adult *Megachile rotundata* (Hymenoptera: Megachilidae). J Econ Entomol 79:974–977

Tepedino VJ, Parker FD (1988) Alternation of sex ratio in a partially bivoltine bee, *Megachile rotundata* (Hymenoptera: Megachilidae). Ann Entomol Soc Am 81:467–476

Tepedino VJ, Torchio PF (1982) Temporal variability in the sex ratio of a non-social bee, *Osmia lignaria propinqua* Cresson: extrinsic determination or the tracking of an optimum? Oikos 38:177–182

Thorp RW, Frankie GW, Barthell J, Gordon D, Newstrom L, Griswold T, Schmidt J, Thoenes S (1992) Ecological research: long-term studies to gauge effects of invading bees. Calif Agric 46:20–23

Torchio PF, Tepedino VJ (1980) Sex ratio, body size and seasonality on a solitary bee, *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae). Evolution 34:993–1003

Trivers RT, Hare H (1976) Haplodiploidy and the evolution of the social insects. Science 191:249–263

Trivers RT, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92

Vila BL, Cassini MH (1994) Time allocation during the reproductive season in vicunas. Ethology 97:226–235

Visscher PK, Danforth BN (1993) Biology of *Calliopsis pugionis* (Hymenoptera: Andrenidae): nesting, foraging, and investment sex ratio. Ann Entomol Soc Am 86:822–832

Wiklund C, Karlsson B (1984) Egg size variation in satyrid butterflies: adaptive vs. historical, "Bauplan" and mechanistic explanations. Oikos 43:391–400

Willmer PG (1986) Foraging patterns and water balance problems of optimization for a xerophilic bee *Chalicodoma sicula*. J Anim Ecol 55:941–962