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MATERNAL AGE CLASS DIFFERENCES IN THE PALLID BAT (*ANTROZOUS PALLIDUS*)  
AND THE TRIVERS-WILLARD SEX RATIO MODEL

The University of Arizona

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IN THE PALLID BAT (ANTROZOUS PALLIDUS)  
AND THE TRIVERS-WILLARD SEX RATIO MODEL

by

Rhonda Marie Sidner

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A Thesis Submitted to the Faculty of the  
DEPARTMENT OF GENERAL BIOLOGY  
In Partial Fulfillment of the Requirements  
For the Degree of  
MASTER OF SCIENCE  
In the Graduate College  
THE UNIVERSITY OF ARIZONA

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STATEMENT BY AUTHOR

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APPROVAL BY THESIS DIRECTOR

This thesis has been approved on the date shown below:

    Russell Davis      
RUSSELL DAVIS  
Associate Professor of General Biology

    21 July 1982      
Date

To Robert William Sidner, Sr.  
who provided an environment rich in  
the right stuff

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## ABSTRACT

Sex ratio adjustment theory (Trivers and Willard 1973) states that females in good condition should produce higher proportions of male offspring than females in poor condition in species for which differential body condition affects reproductive success of males more than females. Before parturition, yearling pallid bats, Antrozous pallidus pallidus, in southern Arizona weigh significantly less than older females despite similar forearm lengths. Assuming greater body weight represents better physiological condition, older females are expected to produce higher offspring sex ratios than yearlings according to the Trivers-Willard model.

No significant differences are found in offspring sex ratios between yearling and older female pallid bats. Most older females produce two young and tend to give birth earlier in the season than yearling females that produce one young. Pallid bats appear to maximize reproductive fitness by adjusting litter size rather than offspring sex.

## INTRODUCTION

Since 1973, much literature has accumulated concerning the Trivers-Willard sex ratio adjustment model. This model is proposed for animals which meet four basic assumptions, and concludes that females in good condition (as indicated by some trait such as body weight) will better their fitness by producing male offspring, while females in poor condition will maximize their fitness by producing female offspring. The rationale for this conclusion is that in species with male competition to fertilize the eggs of many females, good condition males have the potential for greater reproductive success than females in comparable condition (i.e., a poor condition female has a better chance at reproduction than does a poor condition male). The assumptions included in the model are: (1) condition of the young is to some extent dependent on condition of its mother during her period of parental investment; (2) differential conditions in offspring at the end of this period are continued into adulthood; (3) differential condition affects reproductive success of males more than females because of male competition for females in polygynous mating systems; and (4) parents invest equally in offspring of either sex (Trivers and Willard 1973).

In 1930, Fisher described the evolutionary mechanism of natural selection for the sex ratio. He attributed equal sex ratios observed

in nature to equal investment by parents in production of either sex of offspring, because males and females contributed equal halves to the future generation of offspring. Therefore, the primary sex ratio (males:females at conception) is expected to be unity unless parents invest more in a particular sex during the period of parental investment. Such an investment, as defined by Trivers (1972) includes any contribution made to an offspring by its parent which benefits that offspring's chance of future reproduction while preventing the parent from contributing to other offspring. Defense of young from predators and lactation by females are realistic examples.

That sex ratio is genetically controlled and therefore is under evolutionary control by natural selection has been assumed since Darwin (Kolman 1960). Shaw and Mohler (1953) show theoretically that unless differential expenditure by parents for one sex of offspring is occurring, the sex ratio is expected to be unity merely because it is a stable equilibrium value. A simple example is provided by Maynard Smith (1972), although similar examples are found elsewhere (Fisher 1930, Hamilton 1967). If, for instance, females outnumber males in a population, then each male will leave, on average, more offspring than each female. By definition, natural selection will then favor genes producing males. Males will then increase in number to a point that they no longer leave proportionately more offspring than each female, and male-producing genes will no longer be favored.

Adjustment of the offspring sex ratio away from equal numbers of males and females, according to differential physiological condition

of mothers, as suggested above, will not be selected against if the overall population's offspring sex ratio approaches unity. Kolman (1960) has shown through quantification of Fisher's theory (1930) that natural selection acts on the mean sex ratio.

Fisher (1930) and Leigh (1970) carefully explain that when the young of one sex suffer higher mortality than the other sex during the parental investment period, then the former become more expensive to raise in terms of parental effort, but they are cheaper to conceive. This is simply illustrated: If 200 females are born and reared successfully for an arbitrary cost of two parental-effort units each, 400 total parental-effort units are expended. These total units, divided by 200 female young born or 200 young reared, equal two parental-effort units per young conceived or reared. If 200 males are born, but 100 die early, only 100 males are successfully reared for two parental-effort units each. If a cost of one parental-effort unit is assigned to each of the 100 males who died, a total of 300 parental-effort units are expended. Therefore, there are 1.5 parental-effort units per young born (300 divided by 200), but three parental-effort units per young reared (300 divided by 100).

Trivers and Willard (1973) conclude from Fisher's theory that, for mammals, the sex ratio at birth defines the investment by parents in each sex. Deviation from an equal sex ratio indicates differential parental investment in sexes of offspring. This is especially true if sexual dimorphism develops during the period of parental investment causing one sex to make greater demands on the parents (Willson and Pianka 1963).

With species data cited from the literature, Trivers and Willard (1973) note that increased litter size and decreased maternal parity are correlated with decreased maternal investment in offspring. This decreased investment (which they equate with poor maternal condition) is also correlated with lower offspring sex ratios, i.e., fewer males to females (Trivers and Willard op. cit.).

Any polygynous mammalian species that meet the model's assumptions should be appropriate tests of the sex ratio adjustment theory. Pallid bats in southern Arizona, Antrozous pallidus pallidus (Le Conte) (Hall 1981), are robust, 16 to 26 g (Davis 1969a), vespertilionids that appear to have a polygynous mating system and should meet the other assumptions of the Trivers-Willard model. This species was chosen for study because natural differences in body weight are found between groups of females. Davis (1969b) indicates that young and yearling female pallid bats are significantly lighter in body weight than older females when compared at (a) the young's first autumn before entering hibernation, (b) the yearling's first spring after emergence from hibernation, (c) during pregnancy, and (d) into the yearling's second autumn after summer reproductive events.

The present investigation was undertaken to determine if significant differences exist comparing the offspring sex ratios of older pallid bat females with those of yearling females. Yearling females are considered to be in poorer physiological condition than older females, because the yearlings weigh significantly less despite similarity in body size (as measured by forearm length). If adjustment



of offspring sex ratios occurs according to the Trivers-Willard sex ratio model for maternal condition, there should be higher male to female sex ratios among offspring of older pallid bat mothers and lower sex ratios among offspring of yearling mothers, provided that parents are investing equally in either sex of offspring.

To determine if differential parental (maternal) investment in offspring sexes occurs, this study evaluates young pallid bats for sexual dimorphism. Adult pallid bats have been shown to be sexually dimorphic by body weight (Davis 1969b), forearm length (P. Myers 1978), and head-body length (Williams and Findley 1979); however, no such differences have been shown for juveniles during the period of parental investment (Davis 1969b).

In addition, this study compares measurements of young pallid bats by litter size and age of mothers in an attempt to locate decreased maternal investment in relation to litter size and/or condition of the mother. Weight comparisons of maternal pallid bats in relation to their offspring litter size are examined to determine whether differential maternal parity exists.

## MATERIALS AND METHODS

Pallid bats were collected from bridge roosts in southern Arizona near St. David (in 1980, 1981, and early May of 1982) and near Tombstone in 1981. In tables, these roosts are referred to as SD and TB, respectively. Biweekly visits were made to each roost in summer 1981, with weekly visits during a four-week period that included parturition and early development of young. At each visit, all members of a day-roosting colony were captured and examined for sex, reproductive status, general health, and band number. Body weights were measured to the nearest 0.01 g (Ohaus triple beam balance), forearms were measured to the nearest mm (mm ruler), and age was recorded as: a) Young = born that summer (cartilage evident in metacarpal or phalangeal joints); b) Yearling adult = born the summer before (band identification); c) Older adult = born before the previous summer (band identification); and d) New = unknown age but not born that summer (criterion in a). In tables, abbreviations are used for forearm measurements (FA) and body weights (WT).

With the first appearance of young, mother-young associations were recorded at every visit. Mothers with young attached to the nipples were removed from the roost and placed in a separate container. Young were assumed to be those borne by a specific female only if they were found attached to her nipples. After data were recorded for an

isolated mother and young held in a container, these bats were placed in a retaining cage. Such disturbance often resulted in separation of these young and mothers but also provided subsequent opportunity for the reattachment of others. When all bats had been measured, every individual was removed from the retaining cage and placed back into the roost crevice. This provided a chance to recheck mother-young associations. If the only association recorded between a female and young were in the retaining cage, it was not considered a bona fide association. Of 126 females banded at the St. David roost in 1980, only 38 females were recaptured with their 1981 offspring and were used for this study (referred to as Sidner data). Except for two 1980-banded St. David roost females who were recovered at the Tombstone roost during 1981, all other bats captured there were "new" individuals that year. Therefore, age of adults could not be specified, and they were not used in yearling and older female comparisons.

Similar capture and study techniques were used by Davis (pers. comm.) while studying pallid bat maternity colonies in the same area. From his records for four different roosts, studied from 1967 through 1971, data were pooled for 121 known age-class females with mother-young associations to determine offspring sex ratio differences between yearling and older mothers. Forty-three yearling females were counted for 43 yearling mother-young associations. Seventy-eight older females were used to determine 124 older mother-young associations, because these females returned on one or more years. Some females were counted for two, three, or four older mother-young associations. The pooled

data from 1967 to 1971 is referred to as Davis data in the text and tables. Because chi-square analysis revealed no significant differences between the population samples from the Davis and Sidner sets of data for comparisons of offspring sex ratios between yearling and older females, these data sets were pooled for the two variables to form a third data set referred to as combined data. Offspring sex ratio analysis is listed under these three data sets. Other analyses in the text refer to the Sidner data set and include Tombstone unknown-age females where indicated.

Chi-square tests were used to compare offspring sex ratios within and between maternal age classes. Yates correction for continuity was included for chi-square analysis with one degree of freedom (Zar 1974). Two-sample  $t$  tests utilizing pooled variances (Zar 1974) were employed to test differences in forearm lengths and body weights for comparative groups of pallid bats by age, sex, or litter size. For all tests, a probability of 0.05 or less was considered significant.

## RESULTS

### Variation Between Maternal Age Classes

Table 1 lists forearm lengths and body weights of female pallid bats by age class. Comparisons of adult females with juvenile females in late summer and early autumn of the juveniles' first year showed no differences in forearm lengths but did reveal significant differences in body weights ( $P < 0.001$ ). Similar results are shown for comparisons of older adult females with yearling adult females in spring after hibernation and in early summer just prior to parturition. In all these cases, older females were heavier than young and yearling females. However, contrary to Davis' results (1969b), comparisons of the same groups within one week after parturition and again in early autumn (the yearlings' second autumn) showed no significant differences in weight by age class.

Davis (1969b) suggests that older females give birth earlier in the season than yearling females and data from this study supported his view. Parturition in 1981 appears to have occurred during a two-week interval. One young was seen at the Tombstone roost on 9 June. On 16 June, 60% of the 46 females present at the St. David roost had given birth. Of 29 females at Tombstone roost on 21 June, 83% had delivered young. By 23 June, all of the 13 females present at St. David roost had young, the most immature of which had a yearling mother. On 25 June, all 33 females at the Tombstone roost had given birth, but the

Table 1. Forearm Measurements and Body Weights of Female Pallid Bats by Age Class and Time of Year.

Time of Year	OLDER		YOUNGER		<u>t</u>
	N	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	
			<u>JUVENILES</u>		
Summer (Aug)					
1980	FA	73 55.8 ± 1.4 (53-59)	51	56.3 ± 1.7 (53-61)	1.50 <sup>NS</sup>
	WT	73 19.18 ± 1.45 (16.13-21.68)	51	16.25 ± 1.23 (13.96-19.38)	11.74 <sup>***</sup>
Autumn (Sept)					
1981	FA	47 52.2 ± 1.6 (52-60)	24	54.4 ± 2.0 (48-57)	1.81 <sup>NS</sup>
	WT	47 21.06 ± 1.74 (17.65-24.91)	24	16.93 ± 0.98 (15.23-19.64)	10.76 <sup>***</sup>
			<u>YEARLINGS</u>		
Spring (May)					
1982	FA	72 54.9 ± 1.5 (54-59)	16	54.3 ± 1.4 (52-56)	1.48 <sup>NS</sup>
	WT	72 18.04 ± 1.28 (15.03-21.03)	16	16.27 ± 1.40 (14.42-19.24)	4.92 <sup>***</sup>
Summer (June)					
(pregnant)	WT	8 26.68 ± 2.00 (24.22-29.68)	10	22.11 ± 2.26 (17.75-24.02)	4.49 <sup>***</sup>
(within one week after parturition)					
1981	WT	15 19.17 ± 1.90 (14.32-21.82)	8	18.90 ± 1.10 (17.15-20.44)	0.38 <sup>NS</sup>
Autumn (Sept)					
1981	FA	30 54.8 ± 1.1 (53-57)	20	55.8 ± 2.0 (52-60)	2.35 <sup>*</sup>
	WT	30 20.84 ± 1.64 (17.65-23.89)	20	21.61 ± 1.91 (19.03-24.85)	1.52 <sup>NS</sup>

Sample statistics are mean ± standard deviation with range indicated in parentheses. Test statistic is a two-sample t test value comparing body weights (g) or forearm lengths (mm) of older with juvenile or yearling bats.

Statistical significance is indicated at  $\alpha$  (2) level as follows:

NS =  $\underline{P} > 0.05$ , \* =  $\underline{P} < 0.05$ , \*\*\* =  $\underline{P} < 0.001$

young of a yearling mother (a 1980 female from the St. David Roost, recovered throughout 1981 at the Tombstone roost) was not more than two days old as determined by standard aging procedures (Davis 1969b). Of the older females included in Sidner data, 73% had given birth by 16 June. Only 50% of yearlings had borne young by that date.

As expected (Davis 1969b), older females gave birth to a high percentage of twins. Table 2 lists mean productivity of females per age class. Of the births to older females used in this study, 61% were twins; only 3% of the births to yearlings were twins.

#### Sex Ratios Within Maternal Age Classes

Table 2 shows offspring sex ratios within the two age classes of mothers whose offspring had been identified for each of the Sidner, Davis, and combined data sets. Sex ratios were greater than the expected value of unity (i.e., more males:females) for all groups; however, the chi-square test revealed no significant differences.

On 16 and 21 June of 1981, the first days of observing and banding young at St. David and Tombstone roosts respectively, there were more male young present; however, the sex ratios were not significantly different from unity (N = 44 and 46, respectively). These results include some new mothers of unknown age.

For the entire 1981 spring, summer, and autumn periods at St. David roost until 10 October, the total number of young males caught and banded compared with young females differed significantly from a sex ratio of unity (N = 112). The overall young sex ratio at Tombstone roost was not significantly different from one (N = 52).

Table 2. Reproduction and Age Class of Female Pallid Bats.

	YEARLINGS			OLDER		
	Sidner 1980-1981	Davis 1967-1970	Combined Data	Sidner 1980-1981	Davis 1967-1970	Combined Data
Females with assumed offspring	15	43	58	23	124 <sup>1</sup>	147
Total offspring	16	44	60	39	198	237
Offspring/mother	1.07	1.02	1.03	1.70	1.60	1.61
% Twin birth	0.07	0.02	0.03	0.70	0.60	0.61
Total male young	12	24	36	20	107	127
Total female young	4	20	24	19	91	110
Sex ratio (expected 1.0)	3.0	1.2	1.5	1.1	1.2	1.2
Chi-square	3.06	0.21	2.02	0.03	1.14	1.08

See text for explanation of years of data. All chi-square test results show no significant differences between observed sex ratios and expected 1.0 sex ratio.

<sup>1</sup>78 older females were used for 124 birth events. (See materials and methods section for explanation.)



## Parental Investment and Differential Costs of Offspring

### Sexual Dimorphism

Forearm measurements for adult male and female pallid bats are given in Table 3. Data were obtained at the Tombstone roost from adults of unknown ages; however, these animals were at least yearlings in their second autumn. Forearm lengths and body weights were significantly larger for females. Adult yearling females in their first spring were also significantly larger in both traits than yearling males.

Comparisons of male and female juvenile pallid bats at various dates of development are shown in Table 4. These comparisons may include individuals differing in age by as much as three weeks, because most young were not discovered until several days to nearly two weeks after parturition. Estimated age ranges are based upon dates of earliest recorded neonates at these roosts by Davis (1969b) and latest data of neonates discovered in 1981.

Results from Table 4 indicate sexual dimorphism in forearm length and body weight is absent in young pallid bats, at least until after eight weeks of development. By this time females have regressed mammae, and most young have been capable of agile flight (i.e., the parental investment period has ended) for nearly a month. Although there were significant differences in measurements in only two groups after four weeks of age, females tended to have larger forearm lengths and body weight measurements than males. Significant differences were indicated between groups with the largest sample sizes. Forearm measurements of female young of the 16 August sample were not significantly different (Table 1) from adults at the same time.

Table 3. Sexual Dimorphism in Adult Pallid Bats.

	MALES		FEMALES		<u>t</u>
	N	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	
Adults in Autumn (Sept 1981, TB)					
FA	14	53.5 $\pm$ 1.5 (51-56)	32	54.7 $\pm$ 1.5 (52-57)	2.44*
WT	14	19.93 $\pm$ 1.96 (16.75-23.69)	32	20.65 $\pm$ 1.68 (17.40-23.14)	3.03**
Yearling Adults in Spring (May 1981, SD)					
FA	11	52.5 $\pm$ 1.6 (51-56)	16	54.3 $\pm$ 1.4 (52-56)	2.92**
WT	11	14.65 $\pm$ 1.28 (13.14-16.76)	16	16.27 $\pm$ 1.40 (14.42-19.24)	3.05**

Comparisons of forearm length in mm or weight in g by sex and analyzed by two-sample t test. Sample statistics are mean  $\pm$  standard deviation with range in parentheses. Statistical significance assessed at  $\alpha$  (2) level indicated by:

NS =  $\underline{P} > 0.05$ , \* =  $\underline{P} \leq 0.05$ , \*\* =  $\underline{P} \leq 0.01$

Table 4. Forearm Lengths and Body Weights by Sex in Juvenile Pallid Bats.

Date, Roost	MALES		FEMALES		<u>t</u>
	N	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	
16 June, SD ( $<1-1\frac{1}{2}$ wks)					
FA	25	21.9 $\pm$ 3.3 (19-33)	18	21.1 $\pm$ 3.6 (18-31)	0.17 <sup>NS</sup>
WT	25	4.29 $\pm$ 1.06 (2.93-7.34)	18	4.52 $\pm$ 1.44 (2.75-7.93)	0.61 <sup>NS</sup>
21 June, TB ( $<1-2$ wks)					
FA	25	32.6 $\pm$ 5.7 (23-40)	21	30.4 $\pm$ 4.7 (22-39)	1.40 <sup>NS</sup>
WT	25	7.72 $\pm$ 1.79 (4.36-10.55)	21	7.29 $\pm$ 1.74 (4.99-10.74)	0.82 <sup>NS</sup>
23 June, SD ( $<1-2\frac{1}{2}$ wks)					
FA	9	29.4 $\pm$ 4.2 (24-36)	10	29.9 $\pm$ 2.3 (27-33)	0.30 <sup>NS</sup>
WT	9	6.60 $\pm$ 1.57 (4.71-9.27)	10	6.71 $\pm$ 0.65 (5.97-7.76)	0.20 <sup>NS</sup>
2 July, TB ( $1\frac{1}{2}-3\frac{1}{2}$ wks)					
FA	18	44.1 $\pm$ 6.8 (27-51)	17	42.9 $\pm$ 3.9 (36-49)	0.62 <sup>NS</sup>
WT	18	10.64 $\pm$ 2.10 (5.64-13.25)	17	10.68 $\pm$ 1.45 (8.54-13.27)	0.07 <sup>NS</sup>
18 July, TB ( $4-5\frac{1}{2}$ wks)					
FA	19	51.1 $\pm$ 3.0 (46-56)	21	51.7 $\pm$ 2.2 (46-55)	0.68 <sup>NS</sup>
WT	19	13.07 $\pm$ 1.35 (10.07-15.02)	21	13.41 $\pm$ 2.12 (7.58-16.06)	0.98 <sup>NS</sup>
26 July, SD ( $5-7\frac{1}{2}$ wks)					
FA	15	53.0 $\pm$ 2.1 (48-56)	10	53.8 $\pm$ 1.2 (52-56)	1.07 <sup>NS</sup>
WT	15	13.32 $\pm$ 1.61 (9.82-15.25)	10	13.75 $\pm$ 1.11 (11.93-15.71)	0.73 <sup>NS</sup>

Table 4, Continued.

Date, Roost	MALES		FEMALES		<u>t</u>
	N	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	
8 Aug, TB (7-8½ wks)					
FA	21	52.5 ± 1.8 (50-55)	18	53.2 ± 1.5 (50-56)	1.22 <sup>NS</sup>
WT	21	14.97 ± 1.25 (11.85-17.47)	18	15.65 ± 1.62 (11.65-18.11)	1.48 <sup>NS</sup>
16 Aug, SD (8-10½ wks)					
FA	46	55.5 ± 1.5 (52-60)	51	56.3 ± 1.7 (53-61)	2.32*
1980					
WT	46	15.34 ± 1.03 (13.38-17.46)	51	16.25 ± 1.23 (13.96-19.38)	3.97***
21 Aug, SD (8½-11 wks)					
FA	43	55.8 ± 1.7 (50-59)	30	56.5 ± 1.8 (50-59)	1.60 <sup>NS</sup>
WT	43	15.40 ± 1.38 (12.30-18.09)	30	16.12 ± 1.04 (13.65-18.50)	2.42*
18 Sept, SD (12½-15 wks)					
FA	20	53.5 ± 1.4 (51-56)	24	54.4 ± 2.0 (48-57)	1.66 <sup>NS</sup>
WT	20	16.09 ± 1.30 (13.55-18.34)	24	16.93 ± 0.98 (15.23-19.64)	2.44 <sup>NS</sup>
10 Oct, SD & TB (15½-18½ wks)					
FA	9	52.8 ± 1.8 (50-55)	11	53.3 ± 1.8 (49-56)	0.61 <sup>NS</sup>
WT	9	19.78 ± 1.02 (17.90-21.29)	11	20.66 ± 1.74 (17.72-23.25)	1.34 <sup>NS</sup>

All dates for 1981 except 16 August. Statistics and symbols as in Table 3. Estimated age intervals for all individuals in a sample at a roost site are given. Forearm lengths in mm. Weight in g. Statistical significance at  $\alpha$  (2) level indicated by: NS =  $\underline{P} > 0.05$ , \* =  $\underline{P} < 0.05$ , \*\*\* =  $\underline{P} < 0.001$ .

Field notes for the Tombstone roost on 18 July included notations about flight ability of young bats. Later these notations were rated as follows: (1) No true flight; flapping movements or gliding. (2) Disoriented and uncoordinated flight; crash landing; crashing into walls; just capable of hanging up on the night roost wall. (3) Agile flight; capable of clearing obstacles; flying skillfully up and into the day roost crevice without difficulty. Chi-square analysis of this data revealed that flight ability at this stage was independent of sex (Table 5).

#### Litter Size and Maternal Condition

To determine changes in parental investment per offspring with changes in litter size, body weights of young from single births versus twin births were compared (Table 6). As stated previously, almost all twin births were from older mothers, and older mothers tended to give birth earlier in the season than yearling mothers. Therefore, when comparing single with twin young on any date, mean weights for the twin category may be larger merely because they are older. Comparisons of young, therefore, are by dates present, not by precise ages (because most young were not observed soon enough after their birth to determine exact ages). The results during the parental investment period (i.e., before weaning) indicated that young from twin births may be smaller initially but soon equaled or grew larger than single young.

Body weights for 18 July and afterward were not significantly different between young from single births compared with individual

Table 5. Flight Ability and Sex of Young Pallid Bats

Sex	Flight Ability (TB)			Total
	1	2	3	
Male	3	5	12	20
Female	2	5	10	17
				N = 37

See text for explanation of flight categories.

$\chi^2 = 0.14$ , NS

Table 6. Body Weights of Young Pallid Bats From Single Births and Twin Births.

Roost, Date	SINGLE BIRTHS		TWIN BIRTHS		<u>t</u>
	N	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	
SD 16 June	11	4.89 $\pm$ 0.69 (3.73-5.85)	29	4.03 $\pm$ 1.21 (2.75-7.93)	2.21*
26 July	7	13.99 $\pm$ 1.21 (11.93-15.25)	11	12.71 $\pm$ 1.49 (9.82-14.77)	1.90 <sup>NS</sup>
21 Aug	13	16.01 $\pm$ 1.23 (13.76-18.50)	23	15.36 $\pm$ 1.15 (12.30-17.40)	1.59 <sup>NS</sup>
18 Sept	9	17.22 $\pm$ 1.36 (15.15-19.64)	14	16.06 $\pm$ 0.66 (15.23-17.34)	2.75*
TB 21 June	14	6.76 $\pm$ 1.52 (4.36-9.52)	28	7.69 $\pm$ 1.81 (4.96-10.74)	1.62 <sup>NS</sup>
2 July	11	9.71 $\pm$ 2.18 (5.64-12.37)	21	11.13 $\pm$ 1.47 (8.54-13.27)	3.38**
18 July	14	12.84 $\pm$ 1.50 (10.07-15.37)	21	13.12 $\pm$ 1.91 (7.58-15.37)	0.46 <sup>NS</sup>
11 Sept	9	16.40 $\pm$ 1.69 (13.91-19.50)	13	16.70 $\pm$ 1.04 (15.04-18.30)	0.52 <sup>NS</sup>
10 Oct	6	19.64 $\pm$ 1.33 (17.90-21.67)	12	20.36 $\pm$ 1.57 (17.72-23.25)	0.96 <sup>NS</sup>

Statistics as in Table 4. Weight in grams. All samples in 1981.

NS =  $\underline{P} > 0.05$ , \* =  $\underline{P} \leq 0.05$ , \*\* =  $\underline{P} \leq 0.01$

young from twin births. An exception occurred in the 18 September sample but was probably due to one large single young (19.64 g). The t value was not significant when the value was omitted.

The 18 July sample was also the one for which young bats had a wide range of flight abilities. Table 7 shows that flight abilities were also independent of litter size.

Body weights of young from yearling females and from older females were compared (Table 8). A significant difference was found only for the smallest sample size and could be due to sampling error. However, twins were found to be heavier than single young at a corresponding time in the parental investment period (Table 6) and twins are usually the offspring of older females.

Table 9 shows body weights of females who have produced one young that season versus those who produced two young. Results are difficult to interpret because of significant differences found in two samples from the Tombstone roost. For 2 July, in the middle of the lactation period, a difference in body weight may have been understandable. However, no differences were found during the developmental flight period by young, but significant differences were indicated later. No such differences were found at the St. David roost, but samples from times directly comparable to those which were significantly different at the Tombstone roost were not available. Data from both roosts showed no difference in body weights early in the lactation period or at the summer's end. The significant differences found indicated that females who had two young were heavier than females who



Table 7. Flight Ability and Litter Size of Young Pallid Bats.

Litter Size	Flight Ability (TB)			Total
	1	2	3	
Single	2	4	6	12
Twin	3	5	11	19
				N = 31

See text for explanation of flight categories.

$\chi^2 = 0.21$ , NS

Table 8. Body Weights of the Young of Yearling and Older Age Class Pallid Bat Mothers.

Date	YEARLINGS		OLDER		<u>t</u>
	N	$\bar{X} \pm SD$	N	$\bar{X} \pm SD$	
16 June	8	4.33 ± 1.10 (2.93-5.85)	25	4.54 ± 1.35 (2.75-7.93)	0.06 <sup>NS</sup>
23 June	6	7.09 ± 1.84 (4.71-9.27)	12	6.52 ± 0.65 (5.45-7.76)	0.97 <sup>NS</sup>
28 June	5	7.27 ± 1.59 (5.61-9.04)	9	9.01 ± 1.40 (7.19-11.15)	2.13*
26 July	7	13.30 ± 1.93 (9.82-15.25)	11	13.16 ± 1.25 (10.39-14.77)	0.19 <sup>NS</sup>
21 Aug	10	15.55 ± 1.46 (12.30-17.05)	23	15.54 ± 1.20 (13.43-18.50)	0.02 <sup>NS</sup>
18 Sept	5	17.24 ± 1.03 (15.74-18.34)	16	16.29 ± 1.16 (15.15-19.64)	1.64 <sup>NS</sup>

Statistics and symbols as in Table 4. Weight in grams. All samples from St. David Roost in 1981.

Table 9. Body Weights of Female Pallid Bats Who Gave Birth to One Young or Two Young.

Roost, Date	ONE YOUNG		TWO YOUNG		<u>t</u>
	N	$\bar{X} \pm SD$ (range)	N	$\bar{X} \pm SD$ (range)	
SD 16 June	10	19.15 $\pm$ 0.98 (18.12-20.44)	15	18.95 $\pm$ 1.97 (14.32-21.82)	0.30 <sup>NS</sup>
21 Aug	10	19.02 $\pm$ 1.80 (17.07-21.42)	8	18.89 $\pm$ 1.23 (16.45-20.05)	0.43 <sup>NS</sup>
18 Sept	15	21.32 $\pm$ 1.71 (17.82-24.16)	11	20.92 $\pm$ 1.74 (17.65-23.42)	0.58 <sup>NS</sup>
TB 21 June	12	19.30 $\pm$ 1.02 (17.32-21.34)	12	20.02 $\pm$ 1.18 (17.62-21.80)	1.60 <sup>NS</sup>
2 July	16	18.49 $\pm$ 1.21 (15.53-20.35)	15	19.70 $\pm$ 0.91 (17.91-20.98)	3.07 <sup>**</sup>
18 July	15	18.00 $\pm$ 1.16 (15.51-19.87)	7	18.91 $\pm$ 0.62 (18.01-19.76)	1.94 <sup>NS</sup>
8 Aug	13	18.99 $\pm$ 1.06 (16.59-20.53)	10	20.33 $\pm$ 1.14 (17.79-21.69)	2.96 <sup>**</sup>
11 Sept	17	20.29 $\pm$ 1.83 (17.40-23.14)	11	20.95 $\pm$ 1.45 (18.74-22.77)	1.00 <sup>NS</sup>

Statistics as in Table 4. Weight in grams. All samples in 1981.

NS =  $\underline{P} > 0.05$ , \*\* =  $\underline{P} \leq 0.01$

had one young. Therefore, differences in litter size appear to regulate comparable condition (as indicated by body weight) of parous females. This suggests there would be differences in maternal parity if females who maintained weight while producing only one young should instead produce two.

Four yearling females who were found on several occasions in 1981, apparently did not produce young that summer. They never developed enlarged mammae capable of lactation, and of course, they were never found with any young. These four females were significantly lighter-weight in August 1980 than other females of the same age who produced one young in 1981 (when the former-mentioned females were non-productive). The validity of these results is questionable, because of the small sample size ( $N = 4$  and  $9$ ). Forearm lengths between these two groups of females were not significantly different.

Female pallid bats from the Tombstone roost showed a pattern of weight loss after parturition followed by a gradual period of recovery during the time of lactation and developmental flight by young. This pattern was similar to that found by Burnett and Kunz (1982) for Myotis lucifugus and Eptesicus fuscus. For pallid bats the percent weight reduction was not as sharp as those reported by Burnett and Kunz; however, the 21 June date did not give a true initial postpartum weight, because some young were born as early as 9 June. Figure 1 shows that females who bore two young regained their initial postpartum weight sooner than did females who bore only one young. The dashed lines at the Recovery Period indicate time from approximate recovery date until bats were actually observed to have regained initial postpartum body

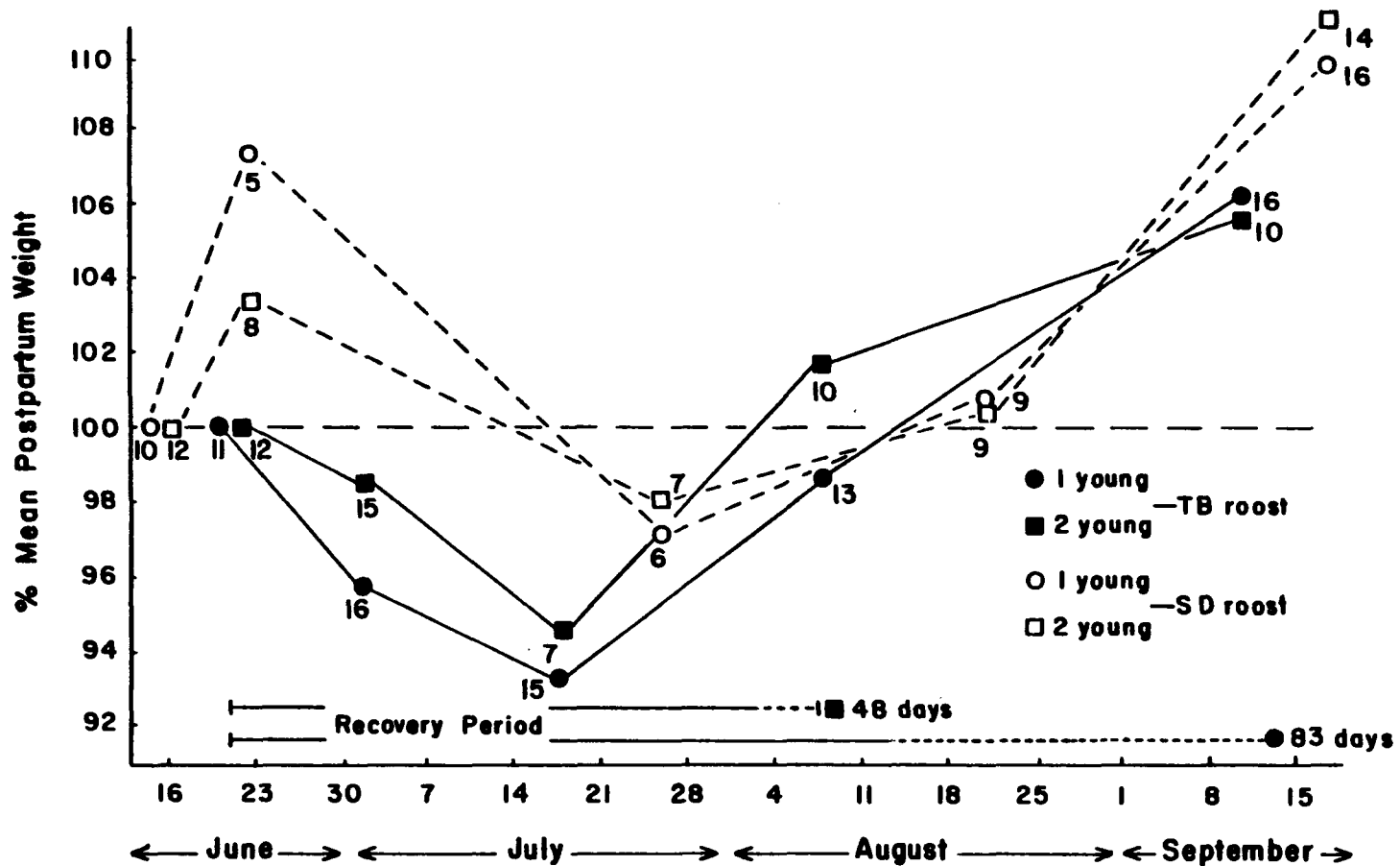


Figure 1. Body Weight Changes of Female Pallid Bats Who Gave Birth to One Young or Two Young. 100% level based on females who had borne young by 16 or 21 June. Mean weights of indicated sample size (numbers below symbols) are expressed as percentages of the mean postpartum weight of females with young by 16 or 21 June. Recovery period is the time interval necessary for females to regain 16 or 21 June postpartum body weight.

weight. Days listed at the Recovery Period state time interval from observation of bats at initial postpartum weight until subsequent observation of bats at regained (initial) postpartum weight. It might seem unusual that a female who had expended energy for two young should have recovered sooner. However, females producing two young were almost exclusively older females. Thus, older females may have been better able to produce and care for two young than yearling females were able to produce and care for one. Unfortunately, postpartum data for females bearing one or two young are for the same initial date. Differential parturition dates for the two groups might yield similar recovery times because older females delivered young earlier in the season and had longer to recover than did yearling females. The recovery period for other species occurs prior to weaning (Burnett and Kunz 1982). Pallid bat mothers did not recover until two or more weeks after weaning. This delay could have been due to the fact that pallid bats are larger than the other species mentioned. Figure 1 also reveals that females at the St. David roost did not show the initial postpartum decrease in body weight. It is not known why this occurred, but small sample sizes and ignorance of actual parturition dates may have been factors contributing to error.

#### Sex Ratios Between Maternal Age Classes

Comparisons shown in Table 10 are for offspring sex ratio differences between the two maternal age classes. Chi-square analysis indicated no significant differences existed in offspring sex ratios between the maternal age classes within each data set.

Table 10. Comparison of Offspring Sex Ratios Between Age Classes of Pallid Bats.

Sex of Offspring	Older	Yearling
Sidner (1980-1981)		
	N = 23	N = 15
Male	20 (0.51)	12 (0.75)
Female	19 (0.49)	4 (0.25)
$\chi^2 = 1.60, NS$		
Davis (1967-1970)		
	N = 124	N = 43
Male	107 (0.54)	24 (0.55)
Female	91 (0.46)	20 (0.45)
$\chi^2 = 0.01, NS$		
Combined Data		
	N = 147	N = 58
Male	127 (0.54)	36 (0.60)
Female	110 (0.46)	24 (0.40)
$\chi^2 = 0.56, NS$		

Chi-square analysis of 2x2 contingency tables to determine significant differences in offspring sex ratios between the age classes. N = number of mothers per age class. Numbers in parentheses are proportions of that sex per total for that age class.

## DISCUSSION

### Sex Ratio Adjustment Reported From the Literature

Discussion of sex ratio adjustment theory necessitates consideration of the sex ratio at various developmental stages in the population. The primary sex ratio is the frequency of males compared to females at conception, the secondary sex ratio is defined at birth, and the tertiary sex ratio is given for times following birth into adulthood (Cavalli-Sforza and Bodmer 1971).

Various mechanisms for adjusting sex ratios have been proposed in the literature (Table 11). Basically, they are of two major types: genetic or gametic; and differential mortality of zygotes, young, or adults. In mammals, where male gametes determine offspring sex, the only means for sex ratio adjustment by females is by selective mortality of sperm, zygotes, or young (Trivers and Willard 1973). It must be remembered that post-fertilization mechanisms by some type of differential mortality, as compared to adjustment before fertilization, results in decreased reproductive potential for the parent (J. Myers 1978). Differential mortality should only occur if the loss of potential offspring benefits other offspring enough to make up for the loss.

Although sex ratio data are often discussed in chiropteran literature, to my knowledge there have been no studies on sex ratio adjustment in bats. If solid evidence is located for differential



Table 11. Mechanisms of Sex Ratio Adjustment Presented in the Literature.

Mechanism	Reference	Explanation
Genetic or gametic mechanisms:		
1. Differential viability or fertilization ability of gametes	Hohenboken 1981	Various attempts to locate meiotic drive mechanisms due to physical or chemical differences between X or Y chromosome-carrying sperm have given some results but most have not been extremely successful. The following experiments are reported in the literature: treatments of semen by density gradient centrifugation, sedimentation electrophoresis, hormones, atmospheric pressure changes, differential pH, selective absorption on ion exchange resins, and cytotoxic antibody reactions in response to Y chromosome histocompatibility antigens. Others reported are: specific estrus-timed insemination, adjusting pH of female reproductive organs, female immunization against Y chromosome histocompatibility antigen.
	Hamerton 1968	It is suggested that not all products of spermatogenesis in structural heterozygotes are equally functional and do not have an equal chance of achieving fertilization. He proposed that with chromosomal changes such as translocations or deletions, chromosomes could gain or lose motility.

Table 11. Mechanisms of Sex Ratio Adjustment Presented in the Literature, Continued.

Mechanism	Reference	Explanation
2. Sex-linked genes	Bryant, Beckenbach, & Cobbs 1982	Traits for SR* determined to be located on the X chromosome in some <u>Drosophila pseudoobscura</u> produce practically all female progeny when males carry the sex-linked X chromosome.
3. Autosomal genes	Bateman 1960	The T locus bearing an autosomal gene (responsible for tail length in house mice) causes selective fertilization by certain sperm of specific allele-bearing eggs.
4. Cytoplasmic inheritance	Cosmides & Tooby 1981	Whereas a 1:1 SR should be favored by autosomal genes for which half come from each sex of parent, this should not be the case for cytoplasmic genes which originate from maternal cytoplasm. They should be selected to produce increased numbers of females in an attempt to increase copies of themselves. This mechanism is named intragenomic conflict.
	Skinner 1982	In <u>Nasonia vitripennis</u> , extrachromosomal factors are inherited through the mother causing the production of all females.

Table 11. Mechanisms of Sex Ratio Adjustment Presented in the Literature, Continued.

Mechanism	Reference	Explanation
Differential mortality of zygotes, young, and adults:		
5. Unguarded X chromosome	Cavalli-Sforza & Bodmer 1971	Originally thought to be one of the major causes of zygotic mortality, the male's X chromosome is unguarded from recessive X-linked lethal traits. Discounting this as a major mechanism of SR adjustment, it is argued that the X-linked lethal recessive is treated as a dominant in males and therefore should be readily selected against resulting in a low frequency of that gene in the population.
	Trivers 1972	If the unguarded X chromosome were a major cause of male mortality, then there should be corresponding mortality in heterogametic female birds. Such is only true for females of certain mating systems of birds.
6. Nutritional deficiencies	Rivers & Crawford 1974	Lab mice show evidence of differential nutritional effects by sex on zygote survival.
7. Behavioral	McClure 1981	Active rejection of offspring alters tertiary SR.

\*SR = sex ratio.

viability and/or meiotic drive mechanisms in mammals, bats could serve as interesting experimental animals because the females of many species can store sperm. If female bats are specialized to the point of having large glycogen granules in the uterine epithelium for nourishment of sperm contained there (Racey and Potts 1970), then perhaps mechanisms could exist for differential selection of gametes.

Diverse and interrelated factors contributing to the maintenance or alteration of the sex ratio are explained in Table 12. One of these factors, local resource competition, may be significant in the biology of pallid bats.

During the summer months, females roost together while storing energy necessary for pregnancy and lactation. Once the young are born, females are constrained by the necessity to supply their young with milk and body warmth, and during this period, time spent away from the roost is less than at other times (Beck and Rudd 1960). Foraging close to the roost would eliminate travel time and permit mothers to spend more time at the roost with young. Therefore local foraging areas could become a limited resource for adult females with young but not for adult males. O'Shea and Vaughan (1977) have shown that male pallid bats do not forage in the same areas as lactating females. Another resource which may be locally-limited, because it is necessary for successful reproduction by females but not by males, is a roost with the specific temperature and other criteria for keeping young warm and preventing excess loss of energy by females through thermoregulation (Vaughan and O'Shea 1976). Males do not share the same roosts with

Table 12. Some Factors Affecting Sex Ratio Reported in the Literature.

Factor	References (with species cited)	Explanation and Comments
1. Physiological condition of mother	Robinette et al. 1957 ( <u>Odocoileus hemionus</u> )	Females produce lower SR* after severe winters than after mild winters. Trivers and Willard (1973) attribute this to the necessity of males in polygynous mating systems to be superior males in order to achieve reproductive success. J. Myers (1978) claims this adjustment is due to the production of the less expensive sex during stressful times if the parent is to maintain a certain quantity of offspring.
	McClure 1981 ( <u>Neotoma floridana</u> )	Food restricted females show differential nestling mortality by sex (more males die) as compared to control diet females.
	Rivers & Crawford 1974 (lab mice)	Experimental females fed a low lipid (essential fatty acid deficient) diet produce decreased litter size due to a decrease in males born.
	Verme 1969 ( <u>Odocoileus virginianus</u> )	For multipurpose females, those underfed produce higher SR than those that are well fed. These results are opposite the other cited examples, but they are complicated by differences in productivity. Those well fed produce more than one young.

Table 12. Some Factors Affecting Sex Ratio Reported in the Literature, Continued.

Factor	References (with species cited)	Explanation and Comments
2. Timing of fertilization in estrus	Verme & Ozoga 1981 ( <u>O. virginianus</u> )	Females mated early in their estrous cycle have a longer time interval from insemination until fertilization and produce a lower SR than those mated late in estrus.
3. Age of mother	Robinette et al. 1957 ( <u>O. hemionus</u> )	Primiparous females produce higher SR than multiparous females. Age of the mother may be influenced by the effect of previous young.
4. Number in present litter	Verme 1969 ( <u>O. virginianus</u> )	As litter size increases from one to four young, the SR decreases.
5. Sex of previous young	Silk et al. 1981 ( <u>Macaca radiata</u> )	When the highest percentage of surviving young are males one year, the following year the SR at birth is high. Following a year of high survival of female young the SR is low.
6. Population density	Snyder 1976 ( <u>Marmota monax</u> )	Experimental removal of approximately half the females in a population one year results in a greatly decreased offspring SR the following year. Similar removal of males results in increased offspring SR. This may be related to stress of increased male aggressions (see #7).

Table 12. Some Factors Affecting Sex Ratio Reported in the Literature, Continued.

Factor	Reference (with species cited)	Explanation and Comments
	Verme & Ozoga 1981 ( <u>Alces alces</u> , <u>Cervus elaphus</u> )	The increase in SR when females are mated late (see #2) in estrus may be due to a decrease in male population density meaning females will wait longer in estrus to mate.
7. Hormones	Geiringer 1961 (lab rats)	Administration of ACTH to pregnant females results in decreased SR. ACTH is released during stress and is postulated to represent the increased aggression present in a population which has an excess of males (see #6). It is hypothesized to affect testosterone production to effect changes in offspring SR.
	Trivers 1972 (lab rats)  ( <u>O. hemionus</u> )	Male rats show higher levels of proteinuria than females but the difference is removed by castration thus implicating androgen as a cause. Males show decreased survival rate caused by protein deficient diet as compared with females. Males show metabolic rate increases over females. It is proposed that this causes susceptibility to disease and injury from aggressive encounters.

Table 12. Some Factors Affecting Sex Ratio Reported in the Literature, Continued.

Factor	Reference (with species cited)	Explanation and Comments
8. Local resource competition	Clark 1978 ( <u>Galago crassicaudatus</u> )	Increased SR is noted for all populations studied. Females compete for limited local resources necessary for successful reproduction. Females remain in an area, while males emigrate to other areas of resources. Therefore the production of female young increases competition for limited resources.
9. Differential expense of young	Fisher 1930	Theory. See introduction.
10. Environmental sex determination	Nichols & Chabreck 1980 ( <u>Alligator mississippiensis</u> )  Charnov et al. 1978 ( <u>Pandalus jordani</u> )	Bipotential-sex young are hatched and sex may be determined by temperature or resource abundance. Heteromorphic chromosomes are lacking (Bull 1980). It is proposed that because sexual maturity is a function of size for females but not for males, resource abundance is more critical for female SR.  The combination of a patchy environment and an individual parent's inability to control which kind of variable environment its offspring will enter are factors favoring environmental sex determination (Charnov & Bull 1977). Individuals born into an environment rich in resources



Table 12. Some Factors Affecting Sex Ratio Reported in the Literature, Continued.

Factor	Reference (with species cited)	Explanation and Comments
		will likely result in large reproductive adults. Because big <u>Pandalus</u> females tend to produce more eggs, it should increase an individual's fitness to become female in such an environment.
11. Local mate competition	Hamilton 1967 (theory - parasitic insects)	In cases where there is not the "Fisher-type" population-wide competition for mates, but rather, competition on a very local level (i.e., on one host upon which eggs are deposited), parents increase fitness by producing just enough sons to fertilize all daughters or all females hatched from another egg clutch at that host. Competition between one's sons does not improve reproductive success.
	Skinner 1982 ( <u>Nasonia vitripennis</u> )	Females alter offspring SR in response to whether their host has been previously parasitized.
12. Inbreeding	Hamilton 1967 (insects & mites)	Many examples are cited for decreased offspring SR when sibmating and arrhenotoky (i.e., production of males by female parthenogenesis) are common characteristics of the species (see #10).

Table 12. Some Factors Affecting Sex Ratio Reported in the Literature, Continued.

Factor	Reference (with species cited)	Explanation and Comments
	Noonan 1978 ( <u>Polistes fuscatus</u> )	Females increase the number of female offspring because inbreeding causes local mate competition between sib-males (see #10).
13. Parental investment and breeding system	Trivers 1972 (theory)	Male aggression and competition (influenced by the particular breeding system) cause changes in the SR due to differential mortality at the tertiary level, and also at the secondary level because sexual dimorphism may cause differential parental investment in offspring by sex.
	Le Boeuf 1978 ( <u>Mirounga angustirostris</u> )	Because of the reproductive fitness value of increased size in adult life, young males try to suckle past weaning from their mother or try to sneak sucklings from other females. This results in injury and mortality.
14. Attractiveness	Burley 1981 ( <u>Poephila guttata</u> )	Sexually dimorphic traits such as color may be judged to represent high quality mates in systems where epigamic selection is important in the breeding system. Females mated with attractive males (based on earlier female preference) produce higher offspring SR than do those mated with unattractive males.

\*SR = sex ratio.

female pallid bats during the period of advanced pregnancy, lactation, and young development; Vaughan and O'Shea (op. cit.) suggest there may be competition for preferred limited roost sites. According to the local resource competition theory (Clark 1978), females should produce more male offspring to decrease the possibility of competition with daughters. This does not appear to be the case for pallid bats.

#### Pallid Bats and the Trivers-Willard Model Assumptions

Consideration of offspring sex ratio adjustment by pallid bats in terms of the Trivers-Willard model requires explanation of the model's assumptions and how they pertain to these bats. The first three assumptions discussed below are stated explicitly by Trivers and Willard (1973) and supported by examples from the literature, although J. Myers (1978) notes the lack of statistical significance in several of the examples cited in the Trivers and Willard paper. A fourth assumption is also included in their paper but is not defined explicitly as such.

1. Condition of the young is to some extent dependent on the condition of its mother during her period of parental investment.

Several lines of evidence from pallid bat data indicated that young were in comparable physiological condition (as measured by body weight) after weaning whether they were from single or twin-producing litters, and whether they had yearling or older mothers.

Young of older females showed no significant differences in body weight from offspring of yearlings (Table 8). However, offspring compared in this study are compared by dates in the season, not by

exact age. Therefore it is possible that twins (usually produced by older females that tended to give birth earlier in the season) were lighter-weight initially but, being one or two weeks older, had gained weight comparable to that of single young (most often produced by yearling females).

Young of single births in some cases were not significantly different in body weight from individuals of twin births (Table 6). At the Tombstone roost, young of single births showed no significant differences from individuals of twin births although one exception indicated heavier twins. Every sample, however, showed a tendency for heavier twins. This finding was consistent with the propensity for twins to be born to older females giving birth earlier in the season. Apparently, in yearling females, either pregnancy is delayed or gestation is prolonged; both suggestions are indications that females are not physiologically able to withstand the energy demands of pregnancy or lactation. Ovulation is delayed in most vespertilionids through hibernation and has been shown to be delayed in pallid bats for various reasons (Orr 1954, Oxberry 1979). Increased length of gestation with negative environmental conditions has been documented for Pipistrellus pipistrellus by Racey and Swift (1981). The results in Table 6 from St. David roost are less easily interpreted, because there the tendency was for heavier single births. There was only one sampling date for the period of maternal investment during which single young were heavier than twin individuals. However, within a week after young were flying (i.e., the end of the parental investment period), there were no

differences in body weights between single and twin individuals. The significant difference in body weight on the earliest date may be explained by twins being lighter-weight thereby decreasing the pregnant female's load, but without detriment to themselves since they had additional time to increase their weight after being born earlier in the season. That young of single births may be initially larger was observed by Brown (1976), although no data was provided in support of the observation. A complicating factor possibly causing heavier single young is the production of one-young litters by older females. Some females may have been just slightly below the minimum physiological condition capable of supporting two young, but well above the capacity to care for one young.

Additional evidence of young ending the parental investment period in comparable condition regardless of single or twin birth was the result that developing flight ability by young bats was not affected by litter size (Table 7). If twins were born earlier, they might have been expected to fly earlier. The absence of differential flight, however, could indicate the need for additional growth time by twins (possible if they were born earlier).

With evidence indicating comparable condition of young bats at the end of the period of parental investment regardless of maternal age class or litter size, it was necessary to look for differences in the condition of the mothers at the end of the period. It has already been stated that young of most older females (whether single or twins) were born earlier in the season; therefore, it appears that older mothers

were physiologically capable of completing pregnancy sooner than yearling mothers. The fact that the majority of older mothers were able to produce two young who were not significantly different in weight from single young provided further evidence that older mothers were in better physiological condition than yearling mothers.

Yearling and older mothers were in comparable condition after parturition and into the autumn (Table 1), a finding contrary to earlier work (Davis 1969b) which showed significant differences in body weight between the age classes of females through the yearlings' second autumn. Finding the similar condition between yearlings and older females at the end of the parental investment period, and the lack of significant differences in body weight at the end of this period between mothers of one or two young (Table 9) was evidence that yearlings and certain older females may only have been able to support a litter of one young. It seems obvious that the young of yearling females or the young of other single-birth mothers would not have done well if their mothers had produced a second young. Results from Table 9 show significant differences on two dates between body weights of single-young and twin-young mothers. In each case, twin-young mothers were heavier; these findings were consistent with the idea that females producing two young had a larger energy need. However, the lack of difference between the two groups at an intermediate sampling date is difficult to understand. The small number of twin-young mothers in the sample may have been a cause, because there is a limited range noticed (Table 9).

2. Differential conditions in offspring at the end of the period of parental investment are continued into adulthood.

Very few returns by males and limited returns by yearlings rendered this assumption practically untestable. However, observations of two of the lightest-weight females in late summer 1980 and again in 1981 indicated some validity for this assumption. One of these females weighed well below the mean on her subsequent capture, and the other gave the minimum weight recorded on five occasions. Very similar results were obtained for two 1981 juvenile females comparing weights just after weaning with attained adult weights the following spring. Similarly, Brown (1976) commented that early individual differences in birth weight and forearm measurements of pallid bats became more pronounced with maturity, but there are no data given to quantify her belief.

3. Differential condition affects reproductive success of males more than females because of male competition for females in polygynous mating systems.

Because colonies of breeding pallid bats and their associated behaviors have not yet been observed other than in the lab (Orr 1954), a consideration of the mating system of these bats can only be conjecture. Many other vespertilionids are assumed to have polygynous or promiscuous mating systems. The fact that many species, including pallid bats (Davis 1969b), have delayed sexual maturity by males could be evidence for selection of better males (Humphrey and Cope 1976). Such a trait could be requisite for epigamic selection and polygynous

breeding. However, conditions which are usually factors contributing to polygynous mating systems are absent in pallid bats: (a) For most polygynous mammals, sexual dimorphism results in males larger than females. However, in pallid bats, females are larger in most measurements than males (Williams and Findley 1979). (b) It would appear that males are unable to monopolize and defend a harem during hibernation because of the energy drain involved in defense. (c) Insects, the food resource of pallid bats, are extremely variable in time and space. It does not seem possible that resource-defense is a strategy for pallid bat breeding.

4. Females invest equally in either sex of offspring.

The absence of significant differences in pallid bat offspring sex ratios from an expected 1:1 sex ratio was evidence of equal investment in offspring sexes. The differences seen in the overall sex ratio (higher proportion of males) of young banded all summer at the St. David roost could be an adjustment to decrease local resource competition (Clark 1978). However, many new juveniles whose mothers were unknown contributed to these overall sex ratios; therefore, the sex ratio differences were probably just due to an excess of stray juvenile males entering the colony.

Sexually dimorphic traits were not evident until after the period of parental investment. This fact was indicative of equal parental investment in either sex of offspring. Differential zygotic or young mortality data were not available to further test this idea.



The development of sexually dimorphic traits (forearm measurement and body weight) in adults and for which female pallid bats were found to be larger, have been hypothesized to be selected traits for the carrying of a large fetus or young in flight (P. Myers 1978). The significant differences seen between juvenile males and females (Table 5) after the parental investment period may have been early reflections of these dimorphic traits.

## CONCLUSIONS

Reflecting upon the assumptions of the Trivers-Willard model and evidence that pallid bats may meet the assumptions, it seems that Antrozous pallidus in southern Arizona does not adjust its offspring sex ratio with maternal conditions as determined by body weight. The offspring sex ratios of each age group (which have been assumed to represent different maternal conditions) were not significantly different from each other.

It appears that pallid bats may alter their maximal reproductive fitness according to maternal condition by adjusting the quantity of offspring rather than the sex.

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