Opportunities for polygyny and reproductive investment in house wrens

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An individual’s fitness depends on both the number and quality of offspring it is able to produce over its lifetime.

Female collared flycatchers with experimentally enlarged broods lay smaller clutches later in life

Experimentally removing second broods increases survival and fecundity the following year in female great tits


For polygamous or multi-brooded species, future costs can be almost immediate if investment in the current reproductive attempt decreases opportunities for additional matings. Under this trade-off we would expect increased opportunities for additional matings to result in decreased investment in the current reproductive attempt.

Male European starlings with a surplus cavity added to their territories contributed less parental care but increased mate attraction efforts (Smith, 1995).

Previous studies have manipulated female investment in current reproduction and demonstrated trade-offs between current and future reproduction... ...ignoring effects of mate choice and paternal investment on female investment.

And shown that male trade-offs between current and future reproduction can be mediated by mate attraction opportunity... ...ignoring effects on female investment in reproduction.
How do opportunities for polygyny affect

1. male investment in current and future reproduction?

2. female mate choice and investment in reproduction?

HOUSE WRENS

North American distribution


BREEDING SEASON

END APRIL
- males return
- establish breeding territories
- start building nests
- females return
- prospect among males
- examine nest sites
- choose male
- complete nest
- lay clutch (5-7 eggs)
- incubate
- both parents provision young

MAY
- maternal investment
- parental investment

JUNE
- young fledge
- second brood

AUGUST
- end of breeding season
How do opportunities for polygyny affect
1. male investment in current and future reproduction?
2. female mate choice and investment in reproduction?

Conceptual framework: male trade-offs between current and future reproduction

Polygyny increases male reproductive success

Availability of surplus cavities affects male opportunity to acquire additional mates

Male parental care affects reproductive success
Conceptual framework: male trade-offs between current and future reproduction

**INVESTMENT IN CURRENT REPRODUCTION**

- **Mate attraction**
- **Parental care**

**INVESTMENT IN FUTURE REPRODUCTION**

- Few opportunities for additional matings

Availability of surplus cavities affects male opportunity to acquire additional mates

Recorded male song for 30 minutes during incubation and nestling periods

Observed paternal provisioning rates during nestling period

Predictions: Male provisioning and mate attraction

During first broods, males with access to surplus cavities will increase mate attraction effort and provision at lower rates relative to males with access to single cavities

Early season nests

- **Male provisioning rate**
- **Male attraction effort**

surplus, single
Male song rates (early season nests only)

Males with surplus cavities in their territories sang more than males with single cavities in their territories.

Post-laying treatment $P < 0.03$
Time × treatment $P < 0.08$

Male provisioning rates (early season nests only)

There were no differences in the proportion of males provisioning nestlings between males with surplus cavities and single cavities in their territories.

Male provisioning rates (early season nests only)

Of males that provisioned, there were no differences in provisioning rates between males with surplus cavities and single cavities in their territories.

Male investment in mate attraction and provisioning effort

- Males with surplus cavities added to their territories
- Sang more during the nestling period but did not provision less than males with single cavities in their territories

1. Trade-offs might occur earlier in the nestling period
   - Male removal studies show that paternal care is most critical when females are brooding young and removal after that period has little effect on reproductive success (Johnston et al. 1992, Bart and Tomes 1989)

2. Provisioning at early season nests might be costly regardless of mate attraction opportunity
   - Males that care for young after they leave the nest are less likely to rear second broods (Bart 1990)
   - Provisioning might be costly if paternal care affects probability of rearing a second brood
Male second broods

First brood provisioning effort

- Provisioned on brood day 12: 56%
- Did not provision on brood day 12: 76%

Proportion of males rearing a second brood

Provisioning rates

More males provisioned late season nests for the entire nestling period than early season nests.

- Male provisioning rates
  - Male second broods

Female investment

- If males provide benefits to females
- Females should preferentially mate with high quality males

- Benefits affect survival or fecundity of females
  - e.g., territory quality (nest site, food availability), parenting ability (provisioning, incubation)

Female house finches gain direct benefits by mating with brightly colored males

- Bright males feed more than dull males

How do opportunities for polygyny affect

1. Male investment in current and future reproduction?
2. Female mate choice and investment in reproduction?
**Female investment**

If males provide **benefits** to females, females should preferentially mate with high quality males. Benefits affect fitness of offspring, e.g., survival (genetic quality), future reproductive success (attractiveness).

**Female barn swallows gain indirect benefits by mating with long-tailed males.** Females mated to long-tailed males have higher reproductive success even though long-tailed males provide less parental care. (Møller 1988, 1994, deLope & Møller 1993)

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**Conceptual framework:**

**Female investment (direct benefits)**

- Availability of surplus cavities affects male opportunity to acquire additional mates
- Polygyny affects male investment in parental care
- Female preferences for males with single cavity territories
- Parental care negatively correlated with surplus cavities
- For females, cavity availability could signal direct benefits

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**Female investment (indirect benefits)**

- Availability of surplus cavities affects male opportunity to acquire additional mates
- Competition among males for high quality territories (more nest sites)
- Female preferences for males with surplus cavity territories
- For females, cavity availability could signal male quality

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**Examples of differential allocation by females**

<table>
<thead>
<tr>
<th>Clutch size</th>
<th>Peafowl</th>
<th>Petrie &amp; Williams (1993)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg size</td>
<td>Mallard</td>
<td>Cunningham &amp; Russell (2000)</td>
</tr>
<tr>
<td>Testosterone in eggs</td>
<td>Zebra finch</td>
<td>Gil et al. (1999)</td>
</tr>
</tbody>
</table>

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**Conceptual framework:**

- Availability of surplus cavities affects male opportunity to acquire additional mates
- Competition among males for high quality territories (more nest sites)
- Female preferences for males with surplus cavity territories
- If there is no trade-off between polygyny and parental care, high quality males might also provide greater parental care
- For females, cavity availability could signal male quality

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**Female investment**

We might expect females mated to preferred males to invest more in reproduction. Differential access and allocation affect fitness of offspring. Higher quality females might have preferential access to preferred males. Females mated to preferred males might allocate more resources to reproduction.
Female investment

- Checked nest boxes to determine date of male territory establishment and female settlement (line date as index)
- Calculated time unmated for each male = measure of female mate choice

- Clutch size as a measure of maternal investment

Predictions: Female settlement/investment

Direct benefits important to females and negative trade-off between polygyny and parental care

Females will preferentially settle with males defending single cavities and females mated to males with single cavities will invest more in reproduction.

Indirect benefits important to females and/or male quality correlated with parental care

Females will preferentially settle with males defending surplus cavities and females mated to males with surplus cavities will invest more in reproduction.

Timing of female settlement (early season nests only)

There was no difference in the time between male arrival and nest lining for males with surplus cavities and single cavities in their territories.
Female investment in clutch size
At early season nests, females mated to males with surplus cavities in their territories laid larger clutches than females mated to males with single cavities in their territories.

![Graph showing standardized clutch size mean ± se for early and late season, with a difference in clutch size between surplus and single cavities, and a P value of < 0.02.]

**Female investment in clutch size**
Perhaps, higher quality females pair with males with surplus cavities. Females mated to males with surplus cavities allocate more to reproduction.

**Female investment in clutch size**
Differential access may arise, allowing access to better males (or territories). Females mated to preferred males might invest more in reproduction.

**Sex ratio manipulation in house wrens**
The Trivers-Willard hypothesis predicts that sex ratios of offspring should be associated with the quality of the parents’ breeding situation. Higher quality females might favor producing more males, as male-biased second broods might yield greater fitness gains than female-biased broods.

**Sex ratio manipulation in house wrens**
In polygynous systems, males in better condition might have higher fitness gains than females in better condition. The reverse might be true under poor conditions.

**Sex ratio manipulation in house wrens**
Females in better condition produce more males, which is due to the production of male-biased second broods.

**Sex ratio manipulation in house wrens**
Females bias the sex of the last-hatched young towards females. Hatching is asynchronous, but fledging is synchronous. The last-hatched young is at a competitive disadvantage relative to its broodmates.

**Sex ratio manipulation in house wrens**
Secondary females bias sex ratios towards females. Second-mated females receive little or no paternal assistance and fledge fewer and lower quality young than first-mated females.

**Sex ratio manipulation in house wrens**
Female blue tits skew the sex ratio of their offspring in response to the UV plumage ornamentation of their mates, a preferred trait and potential viability indicator.
Sex ratio manipulation in house wrens

Females in higher quality breeding situations bias offspring towards sons
females in lower quality breeding situations bias offspring towards daughters

Prediction: Females mated to males with surplus cavities in their territories will bias brood sex ratios towards males

Offspring sex identification

Collected blood samples from nestlings on brood day 12.

Used a PCR-based technique to amplify homologous sections of the CHD-1 gene on the avian sex chromosomes.

females (ZW)       males (ZZ)

[Sexed 247 offspring from 43 early season nests]

Female investment in offspring sex ratios

At early season nests, females mated to males with surplus cavities in their territories produced clutches with higher sex ratios (proportion males) than females mated to males with single cavities in their territories.

Within a brood, male nestlings were larger than female nestlings on brood day 12.

<table>
<thead>
<tr>
<th>MORPHOLOGICAL VARIABLE</th>
<th>Male nestlings</th>
<th>Female nestlings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mass (g)</td>
<td>10.5 ± 0.10</td>
<td>10.2 ± 0.12</td>
</tr>
<tr>
<td>Tarsus (mm)</td>
<td>19.5 ± 0.68</td>
<td>19.2 ± 0.09</td>
</tr>
<tr>
<td>Wing chord (mm)</td>
<td>34.5 ± 0.30</td>
<td>33.9 ± 0.38</td>
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Suggests that the reproductive value of sons and daughters differs for females mated to males with surplus and single cavities.

MANOVA P < 0.03
Female investment in provisioning

There were no differences in per-nestling provisioning rates between females that settled in single cavity and surplus cavity territories.

Female investment in offspring sex ratios

1. Differential access
   Observed sex ratio bias could be due to differences in female condition being correlation with cavity availability
   • Females in good condition might be able to invest in the costlier sex
   • Or good condition sons might have higher reproductive value than good condition daughters

2. Differential allocation
   Observed sex ratio bias could be a response to cavity availability (potential signal of male quality)
   • Females mated to preferred males might invest in sons if attractiveness or viability is inherited from fathers, and those characters influence sons more than daughters.

Both suggest that females prefer males with surplus cavities in their territories

Why would females mated to males with surplus cavities invest more in reproduction but not settle earlier?

1. Nest lining might be a poor index of female settlement date

2. High search costs might risk losing primary status by continuing search secondary females pay high costs of polygyny (Johnson et al. 1993, 1994)

3. Multiple cues used in mate choice and reproductive investment might use other male and/or territory characters in mate choice but cavity availability in investment decisions

Summary

Males with surplus cavities added to their territories sang more during the nestling period

Cavity availability had no effect on paternal provisioning

No demonstrated trade-off between mate attraction and paternal provisioning

• High song rates consistent with mate attraction effort
• Provisioning at early season nests could be costly regardless of cavity availability
• Provisioning effort could be related to male quality, which was randomized across cavity availability
Summary

First brood females mated to males with surplus cavities laid larger clutches and biased offspring towards males. Suggests higher reproductive investment by females settling in territories with surplus cavities.

Females might use cavity availability to assess male quality:
- Higher quality males might have greater access to territories containing surplus cavities (female choice for indirect benefits).
- Higher quality males able to secure territories with surplus nest sites under natural conditions might also contribute more paternal care (female choice for direct benefits).