

ABSTRACT

Title of thesis: BEHAVIORAL ADAPTATION IN THE COURTSIPS
OF SUB-ADULT PLUMAGED MALE SATIN
BOWERBIRDS (*PTILONORHYNCHUS VIOLACEUS*)

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Male satin bowerbirds, *Ptilonorhynchus violaceus*, have complex displays involving multiple display elements that show age-related change over males' first 7 years. Sexual display of sub-adult plumaged (SAP) males with other SAP males appears to allow these males to practice and is of lower quality than that of adult males. In this study we initially attempted to assess age-related changes in SAP male display quality using a female dressed robot. We found that SAP male courtship with female and SAP male dressed robotic birds did not allow us to assess age-related change because these courtships were all of very short duration, much shorter than with live SAP males or courtships by adult males with live or robot receivers. We suggest that because SAP males have low quality displays they are unlikely to attract willing copulations from females who visit their bowers and may thus benefit more from rapid forced copulation than from practicing display with these visitors. Short courtships and copulations with male dressed robots which are rare in natural courtships may result from the failure of our robot to show behaviors that might typically indicate that they are males. These results suggest that SAP males use the behavior of courtship receivers to make decisions about how to respond to birds they court at their bowers.

BEHAVIORAL ADAPTATION IN THE COURTSHIPS OF SUB-ADULT
PLUMAGED MALE SATIN BOWERBIRDS (*PTILONORHYNCHUS VIOLACEUS*)

by

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INTRODUCTION

In many species with non-resource-based (NRB) mating systems, males have complex sexual displays involving multiple traits (Moller and Pomiankowski 1993, Borgia 1995, Höglund and Alatalo 1995). While these traits have been shown to be important in determining adult male mating success (Borgia 1985a,b, McDonald 1989, Zuk et al. 1990 and 1992, Andersson 1994, Gibson 1996, Omland 1996a,b, Andersson et al. 2002, Loyau et al. 2005), we know relatively little about the development of these complex displays. Many studies of display trait development in species with NRB mating systems focus on delayed plumage maturation (Foster 1987, DuVal 2005, Doucet et al. 2007) with less emphasis on the significance of delayed behavioral display acquisition (but see Collis and Borgia 1992 and 1993, Trainer et al. 2002). Studying the development of display can contribute to our understanding of the function of traits in mate choice and thus to our knowledge of the evolution of multiple display traits (see West et al. 2003). In NRB species that demonstrate pronounced delays in male plumage maturation there is evidence that experience plays a major role in the development of effective behavioral display (Collis and Borgia 1992 and 1993, Trainer et al. 2002, Coleman and Borgia MS).

Adult male satin bowerbird (*Ptilonorhynchus violaceus*) displays involve multiple traits that influence mating success including bower quality (Borgia 1985a,b), number and color of decorations (Borgia 1985b, Borgia et al. 1987), display intensity (Patricelli et al. 2002), responsiveness to female signals (Patricelli et al. 2002, 2004, and 2006), and vocal mimicry (Loffredo and Borgia 1986, Coleman et al. 2007). Male behavioral display is similar to male-male aggression display (Borgia and Coleman 2000) and

includes highly synchronized dancing, vocalizations, and vocal mimicry (Loffredo and Borgia 1986). Females prefer intense displays (Patricelli et al. 2002) but males must be responsive to female signals of comfort and adjust their display accordingly to be successful (Patricelli et al. 2006). Studies of display trait development can be important in understanding how males gain skills to develop these complex displays.

Satin bowerbird males go through several age-specific plumage changes such that plumage of 1 to 4 year old males is indistinguishable from that of females, with 5 to 6 year old males showing a transitional dark green neck and ear plumage and their black dark beak changing to yellow (Vellenga 1980, Collis and Borgia 1992 and 1993). We refer to these as sub-adult plumaged (SAP) males because neither group has the adult blue-black plumage of 7+ year old adult males but they are all not clearly juvenile because from age 5 males are able to produce motile sperm (Marshall 1954). SAP males construct temporary bowers (SAP bowers) that are maintained and sometimes shared by one or more males who engage in prolonged same-sex displays (Vellenga 1970, Collis and Borgia 1993, Coleman and Borgia MS). SAP males make uncoordinated movements, change their display intensity suddenly and drastically, do not limit their behavioral display to the bower platform, and mimic poorly (Loffredo and Borgia 1986, Collis and Borgia 1993). Thus, the display of SAP males appears to be of significantly lower quality than that of adult males. The courtship of SAP males by other SAP males appears to provide an opportunity to refine display behaviors important for future mating success (Collis and Borgia 1993, Coleman and Borgia MS). SAP males fail to attract females to their bowers and may attempt to force copulate females courted at the bowers of adult males (Borgia 1986).

The prolonged satin bowerbird maturation period (Vellenga 1980, Collis and Borgia 1992 and 1993) may allow males to practice display behaviors important for future mating success (Collis and Borgia 1993). The initial goal of this study was to investigate in detail how SAP male satin bowerbird display improves with age and compares to the courtship of females by adult males. We could not effectively compare SAP male courtships to adult male courtships directed at females because females do not attend SAP male bowers and because the erratic behavior by the receiving SAP male at SAP male bowers appears to disrupt the courting SAP male's display. Female dressed satin bowerbird robots were courted by adult male satin bowerbirds in successful past experiments (Patricelli et al. 2002, 2006, Savard et al MS). Our plan was to control for these differences by comparing adult male courtships to those directed at female dressed and behaving robotic receivers at SAP male bowers.

Here we report on differences in courtship patterns of SAP and adult males with different kinds of courtship partners including SAP males, female dressed robots, and male dressed robots. Unexpectedly, we found that the SAP male courtships of both female and male robots were extremely short and followed by a copulation attempt. We consider why these different forms of courtship occurred.

METHODS

Observation of courtships

This study was conducted in 2004 at Wallaby Creek, NSW, Australia (Tooloom National Park, see Borgia 1985a). From 31 August through 30 October, individuals were captured using baited traps and fitted with three plastic leg bands arranged in unique color combinations. Hi-8 video cameras that record time and date allowed us to identify leg

band combinations and continuously monitor bird behaviors (Borgia 1995) at 33 contiguous adult bowers and 4 SAP bowers. In addition to SAP males exhibiting courting behavior at some adult bowers, multiple SAP males courted at SAP bowers. Male vocalizations were recorded on camera with an omnidirectional microphone placed 1 meter above the bower platform. Courtships with the female robot were also recorded to verify the identity of the courting male, the display elements performed by each male, and the start and end times of courtship (see below). The following display elements that are common to satin bowerbird courtship were recorded as performed or not performed: short buzzes, ptiloerection, buzz/wing-flips, mimicry of local bird species, and decoration held in beak (Loffredo and Borgia 1986, Patricelli et al. 2002, Coleman et al. 2007). Short buzzes are brief (< 0.20 s) vocalizations performed by males at the beginning of the courtship sequence that encompass a short frequency range (Loffredo and Borgia 1986). Following short buzzes are a series of long buzzes (0.35-1.50 s) coordinated with wing-extensions and running termed buzz/wing-flips (Loffredo and Borgia 1986, Patricelli et al. 2002). Finally, mimicry is performed in which males mimic up to five sympatric bird species: laughing kookaburra (*Dacelo novaguineae*), Lewin's honeyeater (*Meliphaga lewinii*), Australian raven (*Corvus coronoides*), sulphur-crested cockatoo (*Cacatua galerita*), and the yellow-tailed black cockatoo (*Calyptorhynchus funereus*) (Loffredo and Borgia 1986, Coleman et al. 2007).

Female robot experiment

A robotic female satin bowerbird (Patricelli et al. 2002 and 2006) was used at SAP and adult male bowers to experimentally test whether SAP and adult males differ in their courtship of a female. The robot was placed in the bower avenue (see Patricelli et

al. 2002 and 2006). SAP males sometimes court when there is no fully-constructed bower present but a bower platform, a cleared area consisting of layered sticks that is built before the bower walls are constructed. In this case, the robot was placed in the center of the platform. Robot movements were remotely controlled from a blind located at least 6 m from the bower or platform. Control and power wires running from the back of the robot to the blind were buried under leaf litter (see Patricelli et al. 2002 and 2006).

Courtship began when the male arrived on the bower platform and ended when the male attempted copulation with the robot (see Patricelli et al. 2002 and 2006). We calculated the time each male waited before attempting copulation and refer to this as time until copulation (Table 1). When the male arrived on the platform, we lowered the robot to the fully-crouched position where it remained for the entire courtship.

Crouching is a movement from an upright body position to a low body position where the rump is high and the chest is close to the ground (Patricelli et al. 2002). A low crouch position signifies a female's comfort with the male's display, whereas a high crouch position or a startle (a rapid rise out of a low crouch position) indicates wariness (Patricelli et al. 2002 and 2004). We chose to simulate a fully-crouched female so that males would receive the signal that their display was attractive. This avoids the situation where males may see it necessary to adjust their courtship because a mating opportunity is at risk (Patricelli et al. 2006). Also, the robot's head was moved back and forth at a moderate pace to simulate natural female behaviors (Patricelli et al. 2002 and 2006).

Of the 7 adult males and 10 SAP males tested with the female robot, 5 adult male and 8 SAP male courtships were used in the analysis. Two adult males were excluded, one male courted the robot but did not copulate and the other male did not approach the

robot. Two SAP males were excluded because they approached the robot but did not copulate. Two of the 8 SAP males included in the analysis flew directly onto the female robot for an immediate copulation (recorded as 0 s time until copulation). We performed the analysis including and excluding these “fly in” males.

Natural SAP male-male courtship

To examine how SAP male courtship of the female robot compares to natural SAP male-male courtship, we scored video tapes of natural male-male courtships where SAP males from our female robot experiment were the courters. SAP male-male courtship was scored at SAP bowers and at adult bowers that are sometimes used by SAP males when the bower owner is not present. SAP males court other SAP males similarly at SAP and adult male bowers so we combined these data when comparing SAP male-male courtships to SAP male courtships with the female robot. Courtship duration and display elements performed were recorded for each SAP male. If the SAP male courted more than one SAP male receiver (see Table 1), then we calculated the mean duration of his courtships and the mean proportion of courtships in which he performed each display element. Unbanded males were not included in this analysis because they could not be uniquely identified during SAP male-male courtship (see Table 1). The analysis was performed with and without the SAP male who flew directly to the female robot for copulation.

Male robot experiment

We compare SAP male courtship of the female robot to SAP male courtship of a dark-beaked (< 5 years old) SAP male robot. The procedure was the same as that of the female robot experiment, but because this was a preliminary trial we tested this robot in

different crouch positions. In two trials, we positioned the robot upright throughout the courtship. In another trial, the robot was crouched half-way when the SAP male arrived on the platform and remained that way for the entire courtship. Time until copulation and display elements were scored as described above. One SAP male flew directly to the male robot and attempted copulation.

SAP male receiver behavior in natural courtships

To assess whether the male robot is a good representation of receiving SAP male behavior, we quantified SAP male receiver movement in natural courtships by SAP males from our female robot experiment. Since SAP male courtship of the male robot was brief (< 1 minute), each body position change (forward, backward, sideways) by the receiving male was recorded for the first minute of courtship. For SAP males that courted multiple males, the mean number of receiver body position changes was calculated for the first minute of courtship.

Statistical analyses

Non-parametric tests were used due to small sample sizes. The Mann-Whitney U test was used to evaluate the difference between SAP and adult male time until copulation with the female robot. Differences in the proportions of display elements performed were evaluated using Fisher's exact probability test. The Wilcoxon matched-pair test was used for paired comparisons of time until copulation and proportions of courtship elements performed by SAP males from the female robot experiment toward SAP male receivers and the female robot. All tests are two-tailed. Results were considered significant at $\alpha = .05$ and means are presented $\bar{x} \pm SD$.

RESULTS

SAP male versus adult male courtship of the female robot

A robotic female satin bowerbird was used at SAP and adult male bowers to test for differences in SAP and adult male courtship. The proportion of SAP males that performed any display elements during courtship of the female robot was significantly less than that of adult males when fly-in attempts at copulation were included (Table 2). This same pattern was apparent for most display elements when fly-in attempts at copulation were excluded, with the exception of mimicry and decoration in beak. Adult males had much longer courtships ($\bar{x} = 320 \pm 203$ s, $n = 5$) than SAP males with the female robot (including fly-in attempts at copulation (Figure 1): $\bar{x} = 27.9 \pm 38.5$ s, $U = 40$, $z = -2.93$, $n = 8$, $p = .003$; excluding fly-in attempts at copulation: $\bar{x} = 37.2 \pm 40.8$ s, $U = 30$, $z = -2.74$, $n = 6$, $p = .004$). Both categories of SAP males attempted copulation more quickly than adult males when the fly-in attempts at copulation were included (dark-beaked: $\bar{x} = 48.0 \pm 46.7$ s, $U = 20$, $z = -2.45$, $n = 4$, $p = .016$; yellow-beaked: $\bar{x} = 7.75 \pm 14.2$ s, $U = 20$, $z = -2.46$, $n = 4$, $p = .014$), but their mean time until copulation did not differ from each other ($U = 3$, $z = -1.45$, $p = .15$).

SAP male courtship of natural SAP male receivers versus the female robot

We assessed the ability of SAP males from our female robot experiment to perform display in natural SAP male-male courtships by scoring the proportion of display elements performed and courtship duration. The proportion of SAP males performing each display element during natural courtship with other SAP males was significantly higher than that with the female robot when the fly-in attempt at copulation was included (Table 3). When excluding the fly-in attempt at copulation, most display elements

remained significant; however, short buzzes and decoration in beak became insignificant. SAP males from the female robot experiment courted other SAP males in natural courtship longer (including the fly-in attempt at copulation (Figure 2): $\bar{x} = 328 \pm 225$ s, $t = 0$, $z = 2.20$, $n = 6$ pairs, $p = .028$; excluding the fly-in attempt at copulation: $\bar{x} = 332 \pm 251$ s, $t = 0$, $z = 2.02$, $n = 5$ pairs, $p = .04$) than they courted the female robot (including the fly-in attempt at copulation: $\bar{x} = 25.3 \pm 39.3$ s; excluding the fly-in attempt at copulation: $\bar{x} = 30.4 \pm 41.7$ s).

SAP male courtship of the male robot versus the female robot

SAP males performed very few display elements to both the male and female robot (Table 4). Also, the SAP male time until copulation with both the male (including the fly-in attempt at copulation (Figure 3): $\bar{x} = 37.7 \pm 53.6$ s; excluding the fly-in attempt at copulation: $\bar{x} = 56.5 \pm 60.1$) and female robot (including the fly-in attempts at copulation: $\bar{x} = 27.9 \pm 38.5$ s; excluding the fly-in attempts at copulation: $\bar{x} = 37.2 \pm 40.8$ s) was brief. SAP male courtship of the male and female robot appears similar and much less than that of adult males with the female robot but because of the small sample size and variable crouch levels of the robots these data are only suggestive.

Does the SAP male robot provide a good representation of natural SAP male receiver behavior?

We quantified SAP male receiver movement in natural courtships by SAP males from our female robot experiment and compared that to the movement of the male robot to evaluate whether the male robot is a good model of SAP male receivers in natural courtship. We found that receivers in natural SAP male-male courtship made on average 7.7 ± 2.5 body position changes within the first minute of courtship. The male robot was

placed upright (no body position change) in two trials and half-crouched (one body position change) in the other. Therefore, on average we moved the male robot only a third of a body position change when SAP males were courting.

DISCUSSION

SAP males' limited courtship and rapid attempt at copulation with robotic females differed from the adult males who had prolonged courtship before attempting copulation with identical female robots (see also Patricelli et al. 2002 and 2006). The proportion of SAP males presenting display elements in courtships with the female robot was significantly lower than that found by adult males in courtships with the female robot. Most SAP males in these courtships did not include any display elements common to adult satin bowerbird courtship of the female robot. This result is not surprising since SAP courtships were 1/10th as long as the adult courtships. In contrast, we found that SAP males involved in courting the female robot showed very different behavior in natural courtships with other SAP males. Similar to the adult courtship of the female robot, they had long courtships with other SAP males and included display elements seen in adult displays in almost all of their courtships.

One interpretation of these results is that SAP males performed only limited courtship with the robot because they failed to recognize it as a female. This hypothesis is not supported because: First, adult males who are more experienced with courtship and are thus expected to be more able to identify an artificial courtship target court the female robot using longer and more complete displays that do not differ in length from courtships with live females (Patricelli et al 2002). This suggests that adult males treat the female robots as if they are real females. Second, if males were to recognize the

robot as an inappropriate target they should abandon courtship and not pursue copulation. However, we found that SAP males attempt copulation with the female robot quickly often with little or no hesitation. These results suggest that SAP males differ from adult males in their courtship strategy with robotic females and this may reflect differences in how they would react to true females.

The occurrence of limited courtship and rapid copulation in conjunction with the low quality display supports the hypothesis that SAP males attempt rapid and apparently forced copulation because their low quality courtships are unlikely to cause females to remain at the bower long enough to observe courtship and then willingly mate. Adult males are expected to benefit more from presenting prolonged courtship displays because their high quality displays can hold female attention and lead to willing copulations (see Uy et al. 2001). When male satin bowerbirds have a reasonable possibility that they will gain a willing copulation from a female, forced copulation should not be attempted for two reasons. First, there may be little sperm transferred to a female resisting forced copulation. Second, forced copulation limits the male's ability to display his quality to the female and this may cause her to seek copulations with other males that show her an attractive display, possibly resulting in displacement of the first male's sperm that is transferred. Poor quality SAP male displays appear not to be attractive to females, making it unlikely that females would choose to observe prolonged display by SAP males and then copulate with them. Thus, rapid forced copulation may be the most effective reproductive tactic for a SAP male with a female attending his bower, even if his opportunity for reproductive gain is limited because of later copulations by the female with other males.

SAP male courtship of both male and female robots also differs from their natural courtship with other SAP males. The same SAP males who attempted copulation quickly with the female robot engaged in prolonged courtships and included most of the display elements common to adult courtship when they courted live SAP males. The long natural SAP male courtships are consistent with the hypothesis that SAP males court SAP male receivers because they appear to gain from practice with the male when there is no mating opportunity (Collis and Borgia 1993). However, courtships of SAP males with SAP male dressed robots appear more similar to SAP male courtships with female dressed robots than to SAP males in natural courtships. We may have obtained this result because of the design of the robot experiment. First, robots dressed as SAP males had plumage of a young male similar to our robots dressed as females. Second, live SAP male receiver behavior involves a great deal of movement and it seems likely that courting males use the behavior of receivers to determine how they should react to the bird they are courting. If the courted bird shows a great deal of movement they should treat it like the SAP males that commonly attend their bowers and engage in prolonged practice display, but if the receiver remains relatively still, treat it as a female and engage in rapid forced copulation. When we designed the experiments reported here, our goal was to reduce the movement of robots in SAP male bowers in order to measure age-related changes in the quality of SAP male courtships in a way that is comparable to the courtships of adult males. So, rather than mimicking actual SAP male behavior in the bower, we had both sexes of robots perform behaviors more typical of females in adult male bowers. A benefit of this design was our finding, based on the similar treatment of male and female robots, that receiver behavior may be more critical than plumage in

affecting how courting males react to receivers. Erratic SAP male receiver behavior may have originated as a consequence of being frequently startled by the poor quality display of SAP male courtiers. SAP male receivers often return quickly to the bower to observe more courtship and seem less threatened than startled females at adult male bowers who often leave after startles. It is possible that SAP male receivers may have evolved to enhance erratic behavior as a sex specific signal, causing the courting male not to attempt forced copulation and to allow more prolonged courtship from which they both can learn more about how to display.

A remaining question is why, if females do not attend SAP male bowers, males show the seemingly adaptive behavior of attempting forced copulation with our experimental female robots. As we have noted, the female robots in this experiment moved very little as is true of females in adult male bowers which SAP males target for forced copulations. We suspect that SAP males react to motionless receivers in bowers as females whether they are in adult or SAP male bowers. SAP males intruding at adult male bowers often attempt to copulate with females being courted by the adult owners of those bowers. We have no records of females at SAP male bowers so the reaction of these males to the robot may be an artefact of their reaction to motionless females at adult bowers. In fact, if females were to receive courtship at SAP male bowers, the low quality of SAP male courtship may induce females to also have erratic behavior and as such they might not be an immediate target for copulation. This does not occur because unlike SAP males, females have little to gain in the form of learning courtship, and more to lose from possible forced copulations at SAP male bowers.

Several of these comparisons involve relatively few observations because in the year this work was carried out SAP male bowers were rare and relatively ephemeral. Even so, because the behavioral results were dramatically different between experimental tests we were able to obtain significant results from these comparisons. Even with these limitations, our results suggest that SAP males receiving courtship may enhance erratic behavior in the bower to signal their unsuitability as a copulation partner. SAP courters appear to use motionlessness as a signal of an appropriate copulation partner. In future work it would be interesting to include comparisons of male and female dressed robots as courtship receivers to better test the hypothesis that erratic movements are used as a signal of the courtship partner's sex.

Table 1

ID of Courting Male	Male Plumage	Time Until Copulation with Female Robot (s)	Number of SAP male receivers courted
CHP	Dark Beak	18	1
POK	Dark Beak	1	1
SPE	Dark Beak	102	2
XXX	Dark Beak	71	Unbanded
EGL	Yellow Beak	0	7
HLG	Yellow Beak	29	7
LKS	Yellow Beak	2	4
XXX	Yellow Beak	0	Unbanded
EWL	Adult	601	--
KDP	Adult	193	--
KRD	Adult	238	--
LWR	Adult	111	--
MYO	Adult	457	--

Table 1

Identity (ID), plumage, and time until copulation (in seconds) are given for SAP and adult males who courted the female robot. Dark-beaked males are between the ages of 1 and 4 while yellow-beaked males are between the ages of 5 and 7. Additionally, the number of SAP male receivers during natural SAP male-male courtship is given for each SAP male that could be uniquely identified from the female robot experiment.

Table 2

Courtship Element	Proportion of SAP Males (N=8)	Proportion of Adult Males (N=5)	P-value
Short Buzzes	.13	1	.005
Ptiloerection	0	.8	.007
Buzz/wing-flips	0	.8	.007
Mimicry	0	.6	.03
Decoration in beak	.13	.8	.03

Table 2

Fisher's exact probability results for the proportion of courtships where each display element was performed by SAP versus adult males.

Table 3

Courtship Element	Natural Mean Proportion (N=6 pairs)	Robot Proportion	T-value	Z-value	P-value
Short Buzzes	1	.17	0	2.02	.04
Ptiloerection	.9 (.20)	0	0	2.20	.02
Buzz/wing-flips	.99 (.03)	0	0	2.20	.02
Mimicry	.75 (.27)	0	0	2.20	.02
Decoration in beak	.94 (.074)	.17	.16	1.99	.04

Table 3

Wilcoxon matched-pair results for the proportion of courtships where each display element was performed by SAP males in natural courtship versus courtship with the female robot. Standard deviations are given in parentheses for the mean proportions.

Table 4

Courtship Element	Male Robot (N=3)	Female Robot (N=8)
Short Buzzes	.33	.13
Ptiloerection	.33	0
Buzz/wing-flips	0	0
Mimicry	0	0
Decoration in beak	0	.13

Table 4

The proportion of courtships where each display element was performed by SAP males toward the male and female robot.

Figure 1

SAP males attempted copulation with the female robot more quickly than adult males.
Means \pm SD.

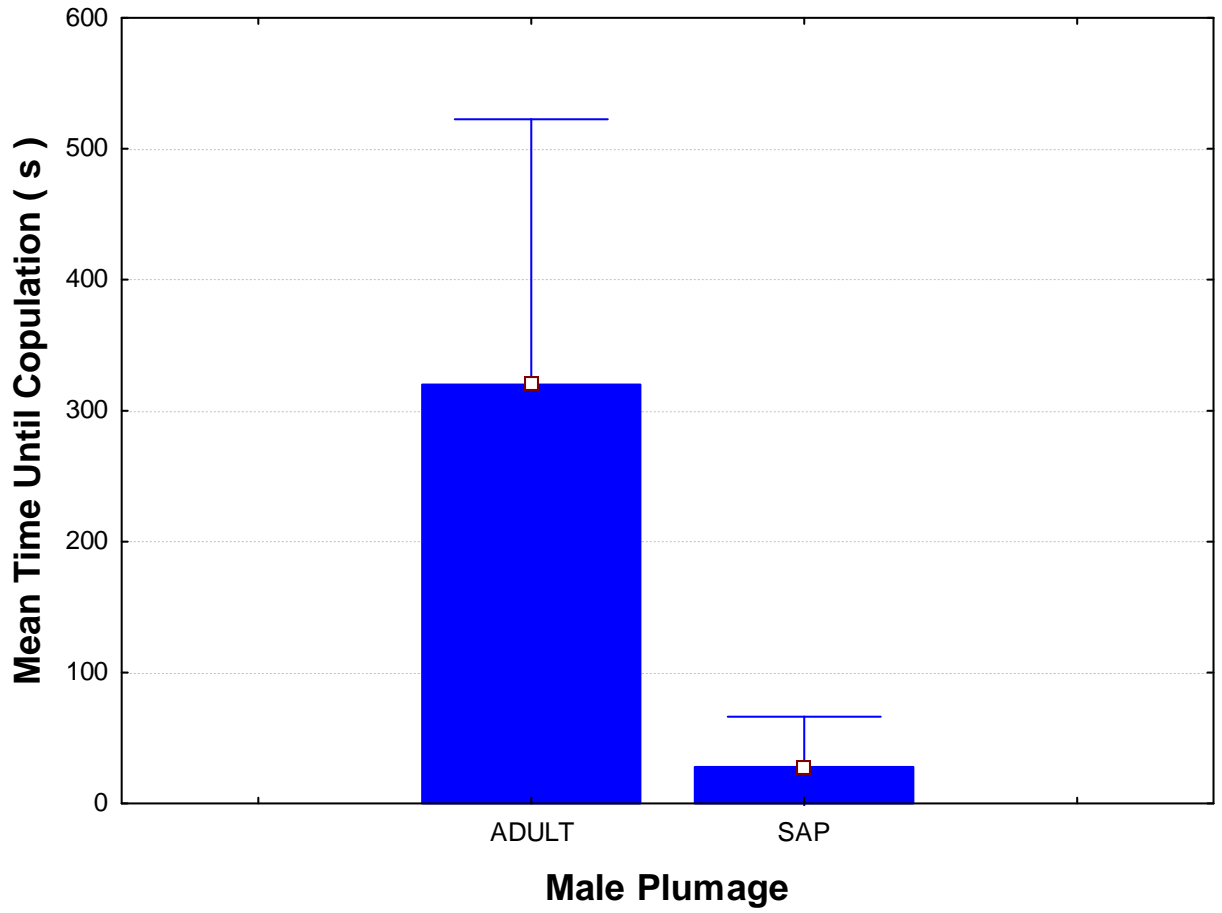


Figure 2

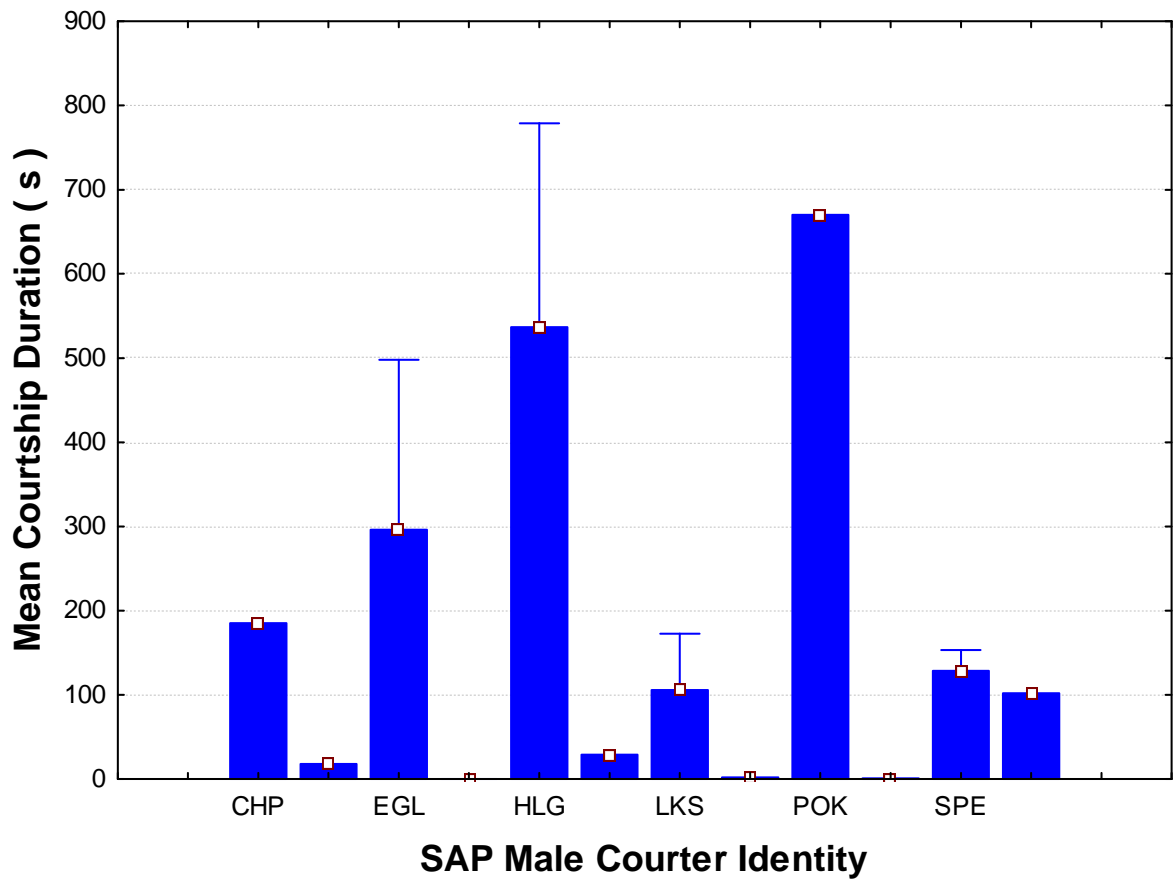
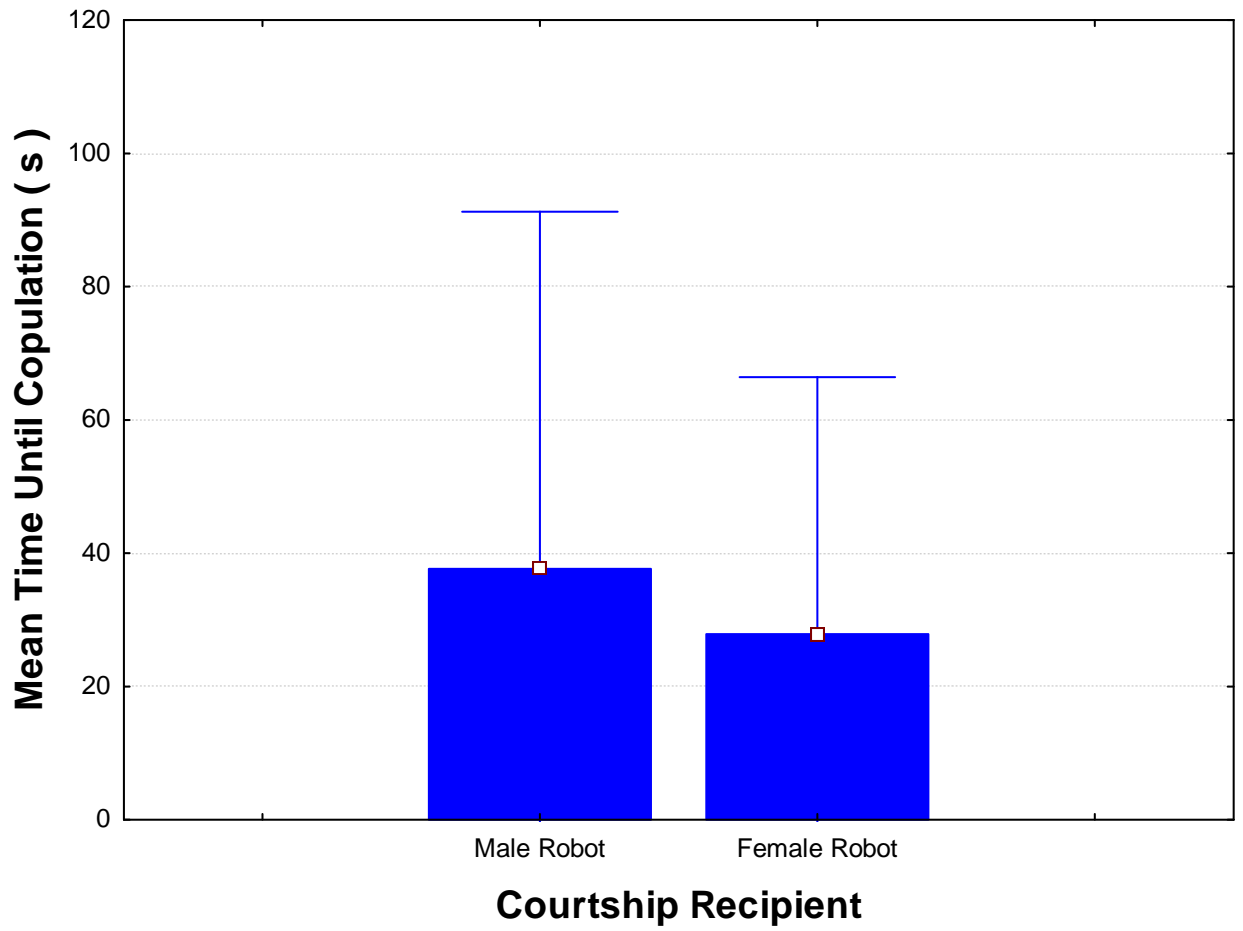


Figure 2

SAP males from our experiment with the female robot courted other SAP males in natural courtship (first bar for each male) longer than they courted the female robot (second bar for each male). EGL flew in for an immediate copulation with the female robot. Means \pm SD for SAP males that courted more than one SAP male receiver.

Figure 3

The mean time until copulation in SAP male courtships of the male versus the female robot. Means \pm SD.



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