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Christopher J. Schell

University of Chicago, cjschell@uw.edu

Julie K. Young

Utah State University, julie.k.young@aphis.usda.gov

Elizabeth V. Lonsdorf

Franklin and Marshall College, elizabeth.lonsdorf@fandm.edu

Jill M. Mateo

University of Chicago, jmateo@uchicago.edu

Rachel M. Santymire

University of Chicago, rsantymire@lpzoo.org

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It takes two: Evidence for reduced sexual conflict over parental care in a biparental canid

CHRISTOPHER J. SCHELL,* JULIE K. YOUNG, ELIZABETH V. LONSDORF, JILL M. MATEO, AND RACHEL M. SANTYMIRE

Committee on Evolutionary Biology, University of Chicago, 1025 E. 57th Street, Culver Hall 402, Chicago, IL 60637, USA (CJS, JMM, RMS)

USDA-WS-NWRC, Predator Research Facility, Department of Wildland Resources, Utah State University, USU – BNR 163, Logan, UT 84322, USA (JKY)

Department of Psychology, Franklin and Marshall College, P.O. Box 3003, Lancaster, PA 17603, USA (EVL)

Davee Center for Epidemiology and Endocrinology, Lincoln Park Zoo, 2001 N. Clark St., Chicago, IL 60614, USA (RMS)

* Correspondent: cjschell@uw.edu

In biparental systems, sexual conflict over parental investment predicts that the parent providing care experiences greater reproductive costs. This inequality in parental contribution is reduced when offspring survival is dependent on biparental care. However, this idea has received little empirical attention. Here, we determined whether mothers and fathers differed in their contribution to care in a captive population of coyotes (*Canis latrans*). We performed parental care assays on 8 ($n = 8$ males, 8 females) mated pairs repeatedly over a 10-week period (i.e., 5–15 weeks of litter age) when pairs were first-time breeders (2011), and again as experienced breeders (2013). We quantified consistent individual variation (i.e., repeatability) in 8 care behaviors and examined within- and among-individual correlations to determine if behavioral plasticity within or parental personality across seasons varied by sex. Finally, we extracted hormone metabolites (i.e., cortisol and testosterone) from fecal samples collected during gestation to describe potential links between hormonal mechanisms and individual consistency in parental behaviors. Parents differed in which behaviors were repeatable: mothers demonstrated consistency in provisioning and pup-directed aggression, whereas fathers were consistent in pup checks. However, positive within-individual correlations for identical behaviors (e.g., maternal versus paternal play) suggested that the rate of change in all behaviors except provisioning was highly correlated between the sexes. Moreover, positive among-individual correlations among 50% of identical behaviors suggested that personality differences across parents were highly correlated. Lastly, negative among-individual correlations among pup-directed aggression, provisioning, and gestational testosterone in both sexes demonstrated potential links between preparental hormones and labile parental traits. We provide novel evidence that paternal contribution in a biparental species reaches near equivalent rates of their partners.

Key words: biparental care, *Canis latrans*, cortisol, coyote, negotiation model, repeatability, sexual conflict, testosterone

Parental care is a necessary yet costly component of reproduction in which individuals invest in offspring at a level determined by their expected future reproductive success (Clutton-Brock 1991; Royle and Smiseth 2012). Although fitness costs and benefits should resolve themselves to produce a single optimum, organisms still demonstrate distinct and consistent individual differences (i.e., personality, repeatability) in their investment (Klug et al. 2012). Repeatability in care behaviors such as provisioning rates (Budaev et al. 1999; Westneat et al. 2013), offspring defense (Wetzel and

Westneat 2014; Stein and Bell 2015), and general offspring contact (Ziegler et al. 2009) differentially affect growth rates, health, and survival of offspring across a population (Storey et al. 2006). Hence, repeatability in parental behaviors may have several consequences for offspring fitness, with reverberating influences on population and ecological structure extending far beyond the individual parent (Bonduriansky and Day 2009; Mousseau et al. 2009). It is therefore imperative to determine the factors associated with individually consistent parental behaviors.

Multiple empirical studies have demonstrated repeatability of parental care in both single-parent (Andersen et al. 2000; Lang et al. 2009; Stein and Bell 2015) and biparental systems (Budaev et al. 1999; Nakagawa et al. 2007; Westneat et al. 2011; Creighton et al. 2014; Wetzel and Westneat 2014). Parenting styles are particularly intriguing for biparental species, in which repeatability may drastically differ for each parent. For instance, individual consistency in provisioning rates (Low et al. 2012) and responsiveness to offspring begging (Lucass et al. 2016) often varies between mothers and fathers. These sex-specific patterns of repeatability may be an artifact of apparent sexual conflict over parental investment, in which one parent of a pair disproportionately benefits from the other parent bearing more reproductive costs (Bebbington and Hatchwell 2015). Alternatively, individual consistency in parenting behaviors occasionally persists within the sexes despite deviation in involvement from either parent (Schwagmeyer et al. 2002; Nakagawa et al. 2007). Regardless, offspring dependence in many biparental species requires involvement of both parents to ensure offspring survival (Lukas and Clutton-Brock 2013; Stockley and Hobson 2016).

Previous studies overwhelmingly focus on avian, insect, or non-mammalian aquatic fauna (Westneat et al. 2011, 2013; Creighton et al. 2014; Stein and Bell 2015). This is most likely because only 5–10% of all mammalian fauna exhibit some level of biparental care (Kleiman and Malcolm 1981; Woodroffe and Vincent 1994). However, parental styles are perhaps more substantial for the evolutionary dynamics of mammals, primarily because parents share intimate and extensive relationships with offspring that often extend for months to years (Maestriperi and Mateo 2009). Such longitudinal associations imply mammalian young are exposed to their parents' styles much longer than other taxa. For these reasons, biparental mammals are prime candidates to explore consistent individual differences in parental care.

Coyotes (*Canis latrans*) are a particularly apt species to address consistent individual differences in parenting and its role in resolving sexual conflict over parental contribution. The species is socially and reproductively monogamous, with mated pairs maintaining exclusive bonds over their lifetime (Hennessy et al. 2012). In addition, pup survival is highly dependent on intensive care from both parents (Sacks and Neale 2001). Given these factors, we may predict the paternal contribution towards care to be relatively congruent with (albeit generally less than) their maternal counterparts (King et al. 2013). Our current understanding of how repeatable variation in care intersects with sexual conflict, however, is lacking empirical support. Further, previous studies have broadly defined the intensity of parental aggressive and affiliative behaviors performed during pup development (Fentress et al. 1987), general parenting patterns in free-living coyote pairs (Bekoff and Wells 1982; Way et al. 2001), and the continued participation of fathers in care (Asa and Valdespino 1998; Sacks and Neale 2001). However, these prior studies lack sufficient data to estimate repeatable variation in the patterns of care.

We addressed 4 major questions in this study that sought to characterize patterns of care and the mechanisms behind

care in coyotes: 1) Do males and females vary in their contribution to care? 2) Does repeatability in care differ by sex? 3) Do mothers and fathers demonstrate similar within- and among-individual correlations? and 4) Is there a link between gestational hormone concentrations and individual consistency in parental behaviors? In a previous study, we demonstrated that concentrations of gestational fecal testosterone metabolites (hereafter referred to as testosterone) of both parents decreased with increasing breeding experience and were repeatable (Schell et al. 2016). We thus predicted that repeatable variation in gestational testosterone would also be linked with parental behavior after parturition in both sexes. Evidence of links between postpartum maternal behavior and preparental hormone levels currently exists for several other taxa (yellow baboons, *Papio cynocephalus*; savannah baboons, *Papio hamadryas* sp.; cotton-top tamarins, *Saguinus oedipus*—Ziegler and Snowdon 2000; Bardi et al. 2004; Nguyen et al. 2008). However, previous work has not decoupled among- and within-individual variances to sufficiently describe covariance among behavioral and hormonal outcomes, particularly in biparental systems. We therefore compare among-individual variances in gestational hormones and latter parental behaviors to assess relationships among labile traits.

MATERIALS AND METHODS

Subjects.—We observed 16 coyotes (8 males and 8 females) from 8 distinct breeding pairs as first-time parents in 2011 and once more as experienced parents in 2013 at the United States Department of Agriculture, National Wildlife Research Center (NWRC), Predator Research Facility in Millville, Utah. Before the onset of our study in 2011, no pairs had prior breeding experience and were all 1 or 2 years of age ($\bar{X} \pm SD = 1.4 \pm 0.1$ years). At the beginning of the breeding season (December), breeding pairs were each placed in 1,000-m² outdoor pens optimized for long-term observations on coyotes (Mettler and Shivik 2007; Gilbert-Norton et al. 2009). Each outdoor pen was also equipped with 2 manufactured PVC den boxes (0.5 m high \times 0.5 m diameter) above ground for coyote use (Brummer et al. 2010). Den boxes were placed into pens before breeding pairs were relocated. These procedures were meant to acclimatize coyotes to the boxes as artificial dens for parturition and rearing. All subjects gave birth in the den boxes, which were readily accessible to NWRC staff. This allowed us to pinpoint offspring parturition date and litter size within 12–24 h.

We observed pups with their parents until early August 2011. Pups were then relocated to outdoor enclosures separate from their natal pens. Pup relocation corresponded to age of dispersal in the wild (Bekoff and Wells 1982). To prevent breeding in 2012, pairs were individually housed over the breeding season, then re-housed as pairs mid-spring. We then observed the same 8 breeding pairs again in 2013 as experienced parents giving birth to their second litters. In 2011, 2 litters were slated for early removal from their natal pens for NWRC-specific projects. From the period between 11 and 15 weeks of age, we

therefore considered 6 litters in 2011 and the full 8 litters in 2013.

Parental care.—We observed parents twice weekly with their litters when offspring were 5–15 weeks of age. We specifically restricted our observational focus between 5 and 15 weeks of pup age because this interval is marked by increased emergence from natal dens, maturation of social skills, and progressive pup weaning (Bekoff and Wells 1982; Fentress et al. 1987; Way et al. 2001). Moreover, we could more feasibly observe parent–offspring interactions during this period because pups were outside den boxes more frequently. Each adult had distinct individual differences in coat pattern, facial features, and tail color. These morphological features were used as a primary means of identification, with adult ear tags and previous shave marks as secondary markers. To reduce coyote wariness, we observed parent–pup units from a mobile observation blind. The blind was a field vehicle familiar to the coyotes at the NWRC and specifically designated for long-term behavioral studies. The blind was parked at a vantage point 50–100 m away from the breeding pair of interest. We used a combination of binoculars and video cameras (Panasonic SD-H85; Panasonic, Shah Alam, Malaysia) to observe coyotes, enabling us to combine live on-site observations with archived video recordings. At any given observation, only 2 individuals were present: 1 who recorded behaviors and another who recorded video. To eliminate inter-observer variation, only a single individual coded behaviors throughout the study. In addition, the 5 video recorders who collected these observations were blind to the individual identity, breeding experience, rearing condition, and age of each animal.

We used a mixed-scan sampling design combining individual and focal group sampling with 1-min intervals and 10-s scan durations (Altmann 1974). Thus, within a 30-min observation period, we noted proximity to pups and general state of each parent (i.e., locomotion versus stationary) at each 1-min interval for a total of 30 intervals. In between intervals, we recorded all-occurrence parenting behaviors (i.e., grooming, carrying, provisioning, pup checks, den checks, pup-directed aggression, and pup-directed play; see Table 1) likely to occur or persist outside of the scan duration. This was done for both mothers and fathers simultaneously. Parental observations occurred over a 30-min period at 0600–0900 and 1800–2130 h, which corresponds to the time of peak activity in the wild (Gehrt and

Riley 2010). We observed each family unit once in the morning and once in the evening per observation week. Thus, each family unit received a total of 60 min of observation per week for 10 weeks in 2011 and 10 weeks in 2013. We used a randomization without replacement design to assign pairs to observation days and times.

Gestational hormone metabolites.—For this study, our goal was to determine whether repeatable variation in cortisol and testosterone metabolites previously observed (Schell et al. 2016) corresponded with subsequent parental care behaviors. To that end, we conducted our analyses using the best linear unbiased predictors (BLUPs) previously reported in Schell et al. (2016). Further details about sample collection, extraction, and analysis can be found in Schell et al. (2016). Briefly, fecal samples were collected 2–3 times per week between January and March with a total of 588 and 689 samples being collected in 2011 and 2013, respectively. Hormone metabolites for cortisol and testosterone were extracted by crushing the sample into a fine powder, agitating the sample with a 90% ethanol mixture, drying down the supernatant, and combining dried supernatants with a phosphate-buffered solution before enzyme immunoassay (EIA). We used a previously validated cortisol EIA to measure coyote fecal glucocorticoid metabolites (Schell et al. 2013). Polyclonal cortisol antiserum (R4866) and horseradish peroxidase were provided by C. Munro (University of California, Davis, California). Cortisol antiserum and cortisol horseradish peroxidase were used at dilutions of 1:8,500 and 1:20,000, respectively. Assay sensitivity was 1.95 pg per well and intra- and inter-assay coefficient of variation was < 10%. We also used a previously established testosterone EIA to measure coyote fecal androgen metabolites (Schell et al. 2016). Testosterone horseradish peroxidase and polyclonal antiserum were used at 1:30,000 and 1:10,000, respectively. Assay sensitivity was 2.3 pg per well and intra- and inter-assay coefficient of variation was < 10% for the testosterone EIA.

Statistical analyses.—We first aimed to characterize mean differences in parenting behaviors between sexes. To that end, we used generalized linear mixed models (GLMMs) fit with a Poisson distribution for count data, and set sex and parity (i.e., first-time versus experienced breeders) as fixed effects in our models. We also included litter size as a fixed effect in our models to assess the potential effect of litter size on parental behavior. Further, data were grouped into 2 previously

Table 1.—Ethogram for parental care assays of coyotes (*Canis latrans*) and the sampling method used to record each behavior. All behaviors were recorded as count data except for proximity and locomote.

Behavior	Description	Sampling method
Grooming	Licks pup	All occurrence
Provisioning	Regurgitates or carries food, or provides milk (mothers) to the offspring	All occurrence
Play	Social interactions (e.g., chasing, leaping, tail wagging, play bows, wrestling) that persist > 5 s with offspring	All occurrence
Aggression	Teeth baring, growling, or shoving directed toward offspring	All occurrence
Den visits	Moves toward and looks directly into den	All occurrence
Pup checks	Sniffs or briefly contacts body of pup	All occurrence
Proximity	Within 5 m of a pup	Instantaneous scan
Locomote	General movement at each scan (e.g., running, walking, trotting); not performed directly to or with pup	Instantaneous scan

described developmental stages (i.e., weaning, 5–10 weeks of age; and juvenile, 10–15 weeks of age—[Bekoff and Wells 1986](#); [Fentress et al. 1987](#)), then included development stage as a fixed effect to determine the influence of pup age on parenting behaviors. Parental identity was set as a random effect in all models. Proximity and locomote were calculated as proportional data and normally distributed as determined by Shapiro–Wilk testing, and thus analyzed using linear mixed models (LMMs) with a Gaussian distribution. Model fit was determined by lowest Δ Akaike Information Criterion (AIC) values ([Burnham et al. 2011](#)).

Our second goal was to quantify repeatability in parenting behaviors. Repeatability is an important index for quantifying the accuracy of measurements and constancy of individual phenotypes over varying environmental conditions and time ([Nakagawa and Schielzeth 2010](#)). Traditionally referred to as the intraclass correlation coefficient, repeatability estimates (R) compare among-individual and residual variance component outputs of mixed regression models to better understand the contribution of individual identity to variance in the data ([Nakagawa and Schielzeth 2010](#)). Here, we calculated repeatability using the rpt function in the rpt.R package ([Nakagawa and Schielzeth 2010](#)), specifying a Poisson distribution with a square root link function for all count variables and a Gaussian distribution for other variables (i.e., proximity and locomote). The rpt function operates using lme4 framework, in which a mixed model and random effect of interest is specified. Variance in litter sizes between mated pairs and across breeding opportunities was considered a potentially confounding variable in our analyses (first-time versus experienced parents, $X \pm SD$: 3.6 ± 1.2 versus 5.4 ± 1.2 pups). We accounted for this variance by including litter size as an additional random effect in the model when estimating adjusted repeatability (R_{adj}) for each behavior. The rpt function then uses a likelihood ratio test framework to produce a P -value, 95% confidence intervals (CI), and standard error (SE) values.

Our third goal was to determine whether within- and among-individual correlations existed across parenting behaviors for each sex, and how those correlations differed between sexes. A univariate model approach was utilized by testing correlations between residuals and individual-level BLUP values ([Sanderson et al. 2015](#)). We used a univariate versus a multi-response mixed-effects model approach primarily because the latter often requires a substantially large sample size ([Dingemanse and Dochtermann 2013](#); [Dosmann et al. 2015](#)). To calculate within-individual correlations across all parenting behaviors, the data were initially parsed into 2 separate datasets for mothers and fathers. Residuals were then extracted from previous GLMMs for each behavior, and Pearson-product moment correlation tests were performed for a total of 28 pairwise comparisons within each sex. To calculate among-individual correlations, coefficients (i.e., BLUPs) were extracted from all GLMMs and LMMs separately for each sex, and correlation tests were again performed for a total of 28 pairwise comparisons per each sex. These same steps were repeated to determine within- and among-individual correlations across the

sexes for identical behaviors (i.e., maternal versus paternal provisioning). A total of 8 pairwise comparisons were made for identical behaviors across the sexes. Though BLUPs are useful in comparing within- and among-individual variation, we do acknowledge that the reported correlations may be artificially low and 95% CI s artificially narrow ([Hadfield et al. 2010](#)). Consequently, we express caution in our discussion as to the significance of reported correlations.

Our final goal was to assess among-individual correlations in gestational hormones and parental care behaviors. A univariate model approach was used once more by testing correlations among individual-level BLUPs. BLUP values for hormones were previously reported in [Schell et al. \(2016\)](#). Correlation tests were performed for a total of 16 pairwise comparisons within each sex.

All statistical analyses were performed using R version 3.3.2 ([R Core Team 2017](#)). All GLMMs and LMMs were performed using the glmer and lmer functions (i.e., proximity and locomote; [Table 1](#)) from the “lme4” package ([Bates et al. 2012](#)). We used restricted estimation maximum likelihood with a diagonal covariance structure for all our models. Repeatability estimates, SE s, and associated 95% CI s were computed using the rpt function from the rpt.R package ([Nakagawa and Schielzeth 2010](#)). Extraction of residuals and BLUPs for within- and among-individual correlations, respectively, were performed using the residuals (resid()) function, and the coef() function built into the R framework ([R Core Team 2017](#)). Pearson correlation tests and accompanying CI s were computed using the cor.test function, and the significance of all P -values was assessed before and after Bonferroni corrections. In all cases, we used 2-tailed tests with alpha set to $P < 0.05$ and data reported as mean $\pm SE$. We used Shapiro–Wilk tests for all data to determine normality before analyses.

RESULTS

In total, we observed parents for approximately 160 h over 20 weeks with 10 h of observation for each coyote. We performed an initial assessment of how well each fixed and random effect (i.e., individual identity as the intercept) approximated variance in care behaviors by using slope estimates and SE s from all GLMMs and LMMs ([Fig. 1](#)). The primary purpose was to determine the overall influence of litter size on our results. Breeding experience (i.e., parity) was a better explanatory variable compared to litter size in approximating variation in pup-directed aggression, provisioning, and pup checks. For all other behaviors, either the developmental period or intercept terms more appropriately approximated these data ([Fig. 1](#)) compared with litter size.

Do males and females vary in their contribution to care?—Mothers and fathers varied minimally in their mean contribution to care ([Table 2](#)). Within the weaning period (i.e., 5–10 weeks of litter age), mothers provisioned pups more than fathers ([Table 2](#)). During the juvenile period (i.e., 11–15 weeks of age), mothers played with and checked on their pups more frequently as well ([Table 2](#)). Mothers and fathers did not significantly

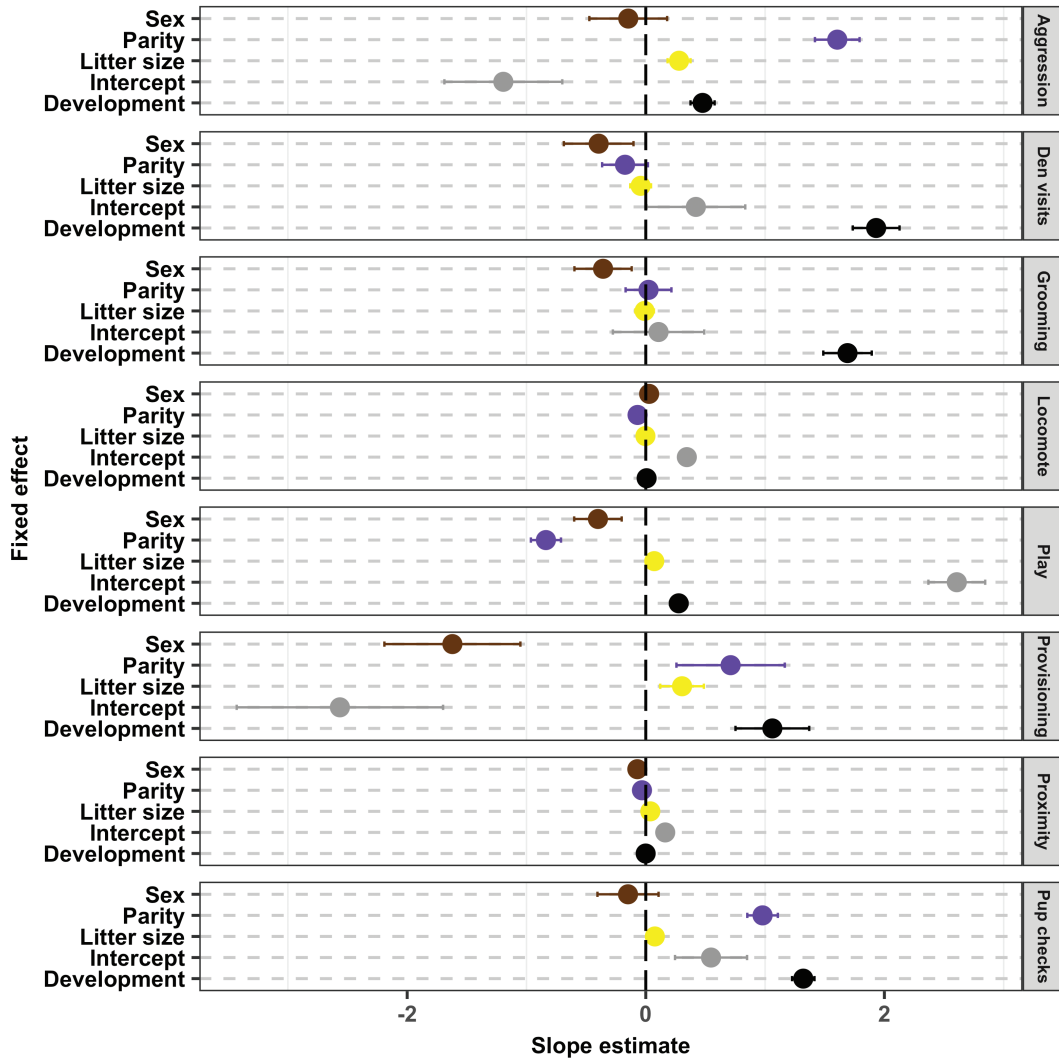


Fig. 1.—Slope estimates and *SEs* of all potential fixed effect terms (left of each panel) for each of the observed parenting behaviors (indicated on the right side of the panel) of coyotes (*Canis latrans*). The distance above zero determines how proficient each fixed effect is at approximating variance within the data relative to other fixed effects. The intercept term denotes the contribution of individual identity to the expression of each behavior. Each fixed effect term is further delineated by color (Sex = brown; Parity = purple; Litter size = yellow; Intercept, i.e., Animal identity = gray; and Developmental period = black).

differ in their rates of any other parental behaviors in either developmental period. Across developmental periods, mothers and fathers exhibited reductions in the number of grooming (mothers: $z = -5.633$, $d.f. = 14$, $P < 0.001$; fathers: $z = -4.745$, $d.f. = 14$, $P < 0.001$), den visits (mothers: $z = -9.709$, $d.f. = 14$, $P < 0.001$; fathers: $z = -6.723$, $d.f. = 14$, $P < 0.001$), and pup checks performed (mothers: $z = -3.027$, $d.f. = 14$, $P = 0.002$; fathers: $z = -3.562$, $d.f. = 14$, $P < 0.001$) from the weaning to juvenile developmental period. In addition, mothers demonstrated reductions in provisioning ($z = -2.652$, $d.f. = 14$, $P = 0.008$) and increased pup-directed play ($z = 2.751$, $d.f. = 14$, $P = 0.006$) over developmental time, whereas fathers exhibited reductions in pup-directed play ($z = -4.541$, $d.f. = 14$, $P < 0.001$). Females demonstrated more aggressive displays ($z = 3.843$, $d.f. = 14$, $P < 0.001$), pup checked ($z = 2.567$, $d.f. = 14$, $P = 0.010$), and den visited ($z = 2.899$, $d.f. = 14$, $P = 0.004$) their offspring more frequently as experienced versus first-time mothers. Males

also increased the number of pup-directed aggressive displays ($z = 3.048$, $d.f. = 14$, $P = 0.002$) as experienced versus first-time parents. For all reported behaviors, litter size was only a significant effect for males, specifically, fathers with larger litters generally visited pups at the den more frequently ($z = 2.310$, $d.f. = 14$, $P = 0.021$) and spent more time close to their offspring ($t = 2.656$, $d.f. = 14$, $P = 0.024$). Further interaction effects between parity and developmental period can be found in Supplementary Data SD1.

Does repeatability in care differ by sex?—Mothers demonstrated repeatability in provisioning, pup-directed aggression, and locomotion (Table 3). Comparatively, fathers were repeatable in pup checks and locomotion (Table 3). Neither sex was repeatable in any other care behavior observed.

Do mothers and fathers demonstrate similar within-individual correlations?—Mothers demonstrated positive within-individual correlations for approximately 75% of all possible

Table 2.—Results of generalized linear mixed models comparing maternal and paternal all occurrence and instantaneous scan parenting behaviors of coyotes (*Canis latrans*) within each developmental period. Bolded values indicate significant differences between mothers and fathers ($P < 0.05$). Proximity and locomotion measures were normally distributed, and we therefore used linear mixed models. F -statistics are reported for instantaneous scan behaviors (proximity 5–10 weeks: $F_{(1,13.7)}$; 11–15 weeks: $F_{(1,12.2)}$; locomote 5–10 weeks: $F_{(1,12.9)}$; 11–15 weeks: $F_{(1,13.9)}$) with the corresponding P -values).

Behavior	Mothers	Fathers	z	P
5–10 weeks				
Grooming	6.19 ± 0.94	4.44 ± 0.98	−1.318	0.188
Provisioning	2.38 ± 0.71	0.25 ± 0.14	−3.080	0.002
Play	17.31 ± 3.52	13.75 ± 2.13	−0.770	0.441
Aggression	9.44 ± 4.46	6.44 ± 2.62	−1.003	0.316
Den visits	8.75 ± 1.64	6.44 ± 1.36	−1.153	0.249
Pup check	16.31 ± 2.52	19.375 ± 5.12	−0.158	0.847
Proximity	31.18 ± 2.56%	25.13 ± 2.31%	2.681	0.124
Locomote	30.00 ± 3.00%	33.00 ± 4.00%	0.401	0.538
11–15 weeks				
Grooming	1.21 ± 0.39	0.79 ± 0.26	−0.773	0.440
Provisioning	0.64 ± 0.27	0.36 ± 0.17	−1.054	0.292
Play	15.14 ± 3.29	7.29 ± 1.67	−2.038	0.042
Aggression	6.21 ± 2.07	4.86 ± 1.50	−0.031	0.976
Den visits	1.21 ± 0.43	0.86 ± 0.39	−0.987	0.323
Pup check	6.43 ± 1.19	3.64 ± 0.90	−2.043	0.041
Proximity	32.82 ± 3.36%	24.16 ± 3.58%	−4.197	0.063
Locomote	28.00 ± 3.00%	30.00 ± 4.00%	0.080	0.781

Table 3.—Adjusted repeatability estimates (R_{adj}), SE s, low and high 95% CI limits, and associated P -values for parenting behaviors of coyotes (*Canis latrans*) in mothers and fathers. Bold values indicate significant repeatability estimates.

Behavior	R_{adj}	SE	Low CI	High CI	P
Mothers					
Grooming	0.000	0.056	0.000	0.150	1.000
Provisioning	0.575	0.189	0.203	0.762	0.012
Play	0.000	0.104	0.000	0.246	0.500
Aggression	0.423	0.277	0.048	0.827	0.003
Den visits	0.000	0.068	0.000	0.174	0.500
Pup checks	0.000	0.068	0.000	0.170	1.000
Proximity	0.327	0.189	0.058	0.628	0.120
Locomote	0.551	0.157	0.289	0.778	0.004
Fathers					
Grooming	0.115	0.224	0.000	0.583	0.304
Provisioning	0.314	0.165	0.000	0.436	0.169
Play	0.244	0.261	0.000	0.761	0.051
Aggression	0.030	0.221	0.000	0.568	0.452
Den visits	0.394	0.214	0.038	0.625	0.061
Pup checks	0.603	0.300	0.017	0.818	0.003
Proximity	0.000	0.005	0.000	0.013	1.000
Locomote	0.518	0.192	0.166	0.713	0.014

pairwise comparisons, with 67% of those correlations still significant after Bonferroni correction (Table 4). The rate of decrease in maternal provisioning, for instance, corresponded with decreased aggression and pup checks over developmental time. Similarly, the rate of maternal-induced play bouts decreased with proximity and pup checks with increasing developmental time (Table 4). Comparatively, fathers demonstrated positive within-individual correlations for approximately 68% of possible comparisons, with 84% of those correlations still significant after Bonferroni correction (Table 4). Of the 21 within-individual correlations mothers demonstrated, their male counterparts exhibited approximately 76% of the same positive correlations. Moreover, mothers and fathers demonstrated positive

within-individual correlations for all identical behaviors except provisioning (e.g., maternal versus paternal grooming; Fig. 2). In sum, changes in the rate of behaviors within and between mated partners co-occurred with increasing developmental time. See Supplementary Data SD2 and SD4 for fully annotated results from univariate mixed models and correlation tests.

Do mothers and fathers demonstrate similar among-individual correlations?—Mothers demonstrated positive among-individual correlations for approximately 79% of all possible pairwise comparisons, with 45% of those correlations significant after Bonferroni correction (Table 5). For instance, mothers with high provisioning personalities also tended to be aggressive and attentive mothers (i.e., greater den visits, pup checks, proximity;

Table 4.—Within-individual correlations (r_p) among parental care behavior of coyotes (*Canis latrans*) with 95% CIs (low CI and high CI), partitioned by (a) mothers and (b) fathers. For all behavior, we obtained 10–20 measurements per individual on 16 coyotes (8 mothers and 8 fathers) for a total sample size of 305 measurements ($d.f. = 303$). Bolded values denote significant correlations after Bonferroni correction for multiple comparisons. See Supplementary Data SD2 for specific correlation and covariance estimates, t -values, and P -values.

	Grooming	Provisioning	Play	Aggression	Den visits	Pup checks	Proximity
(a) Mothers							
Provisioning	0.070 (−0.04, 0.18)						
Play	0.204 (0.09, 0.31)**	0.095 (−0.02, 0.21)					
Aggression	0.281 (0.17, 0.38)***	0.200 (0.09, 0.31)***	0.233 (0.12, 0.34)***	0.038 (−0.07, 0.15)			
Den visits	0.192 (0.08, 0.30)***	0.122 (0.01, 0.23)*	0.058 (−0.05, 0.17)	0.177 (0.07, 0.28)**	0.158 (0.05, 0.27)**		
Pup checks	0.463 (0.37, 0.55)***	0.143 (0.03, 0.25)*	0.320 (0.22, 0.42)***	0.268 (0.16, 0.37)***	0.008 (−0.10, 0.12)	0.294 (0.19, 0.39)***	
Proximity	0.317 (0.21, 0.42)***	0.071 (−0.04, 0.18)	0.445 (0.35, 0.53)***	0.134 (0.02, 0.24)*	0.341 (0.24, 0.44)***	0.368 (0.27, 0.46)***	0.021 (−0.09, 0.13)
Locomote	0.199 (0.09, 0.30)***	0.139 (0.03, 0.25)*	0.163 (0.05, 0.27)**				
(b) Fathers							
Provisioning	0.196 (0.09, 0.30)***						
Play	0.315 (0.21, 0.41)***	0.083 (−0.03, 0.19)	0.226 (0.12, 0.33)***	0.067 (−0.05, 0.18)			
Aggression	0.248 (0.14, 0.35)***	0.064 (−0.05, 0.17)	0.228 (0.12, 0.33)***	0.193 (0.08, 0.30)***	0.187 (0.08, 0.29)**		
Den visits	0.170 (0.06, 0.28)**	0.030 (−0.08, 0.14)	0.350 (0.25, 0.44)***	0.312 (0.21, 0.41)***	0.193 (0.08, 0.30)***		
Pup checks	0.311 (0.21, 0.41)***	0.187 (0.08, 0.29)**	0.489 (0.40, 0.56)***	0.073 (−0.04, 0.18)	0.142 (0.03, 0.25)*	0.341 (0.24, 0.44)***	
Proximity	0.367 (0.27, 0.46)***	0.157 (0.05, 0.26)**	0.128 (0.02, 0.24)*			0.375 (0.27, 0.47)***	0.044 (−0.07, 0.16)
Locomote	−0.012 (−0.12, 0.10)	0.084 (−0.03, 0.19)					

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Table 5). Comparatively, fathers demonstrated positive among-individual correlations for approximately 57% of all possible pairwise comparisons, with 38% of those comparisons significant after Bonferroni correction (Table 5). Of the 22 among-individual correlations mothers displayed, their male counterparts exhibited approximately 68% of the same positive correlations. Moreover, maternal and paternal BLUPs for identical behaviors were positively associated for grooming, provisioning, aggression, and den visits (Fig. 2). Hence, mothers with highly attentive care personalities were matched with highly attentive fathers. See Supplementary Data SD3 and SD4 for fully annotated results, specifically correlation and covariance estimates, 95% CIs, t -values, $d.f.$, and P -values.

Is there a link between gestational hormone concentrations and individually consistent parental behaviors?—Females with consistently high cortisol during gestation were low-grooming and less aggressive mothers postpartum (Fig. 3). High-cortisol females had higher proportions of locomotor activity during pup development (Fig. 3), although these relationships were not significant after Bonferroni correction. Further, females with consistently high gestational testosterone were consistently playful mothers, whereas they tended to provision and perform aggressive displays to their pups less frequently (Fig. 4).

Males with consistently high gestational cortisol also visited their dens more frequently as fathers (Fig. 3), although this trend was not significant after Bonferroni correction. High-testosterone males groomed, provisioned, acted aggressively toward, visited, and checked on their pups less frequently (Fig. 4). Negative among-individual correlations among paternal gestational testosterone and provisioning, aggression, and den visits remained significant after Bonferroni correction. Finally, males with consistently high gestational testosterone had higher proportions of locomotor activity postpartum (Fig. 3). See Supplementary Data SD5 for fully annotated results, specifically correlation and covariance estimates, 95% CIs, t -values, $d.f.$, and P -values.

DISCUSSION

In biparental systems, partners should contribute at near-equal rates to reduce sexual conflict over parental investment (King et al. 2013). Here, we found that coyotes do indeed reduce sexual conflict and demonstrate similar mean contribution of care between mothers and fathers. However, there were distinct differences in which behaviors were repeatable in both sexes. In fact, several within- and among-individual relationships persisted after controlling for variance in litter size and multiple comparisons. Further, we provide evidence to suggest potential links among gestational cortisol, testosterone, and later care behaviors in both sexes.

The avian literature is replete with examples of repeatability and coordinated care between mated individuals (Schwagmeyer et al. 2002; Johnstone and Hinde 2006; Nakagawa et al. 2007; Meade et al. 2010; Johnstone 2011; Schuett et al. 2011; Low et al. 2012; Wetzel and Westneat 2014; Bebbington and Hatchwell 2015). However, offspring of mammalian mothers gestate internally and are dependent

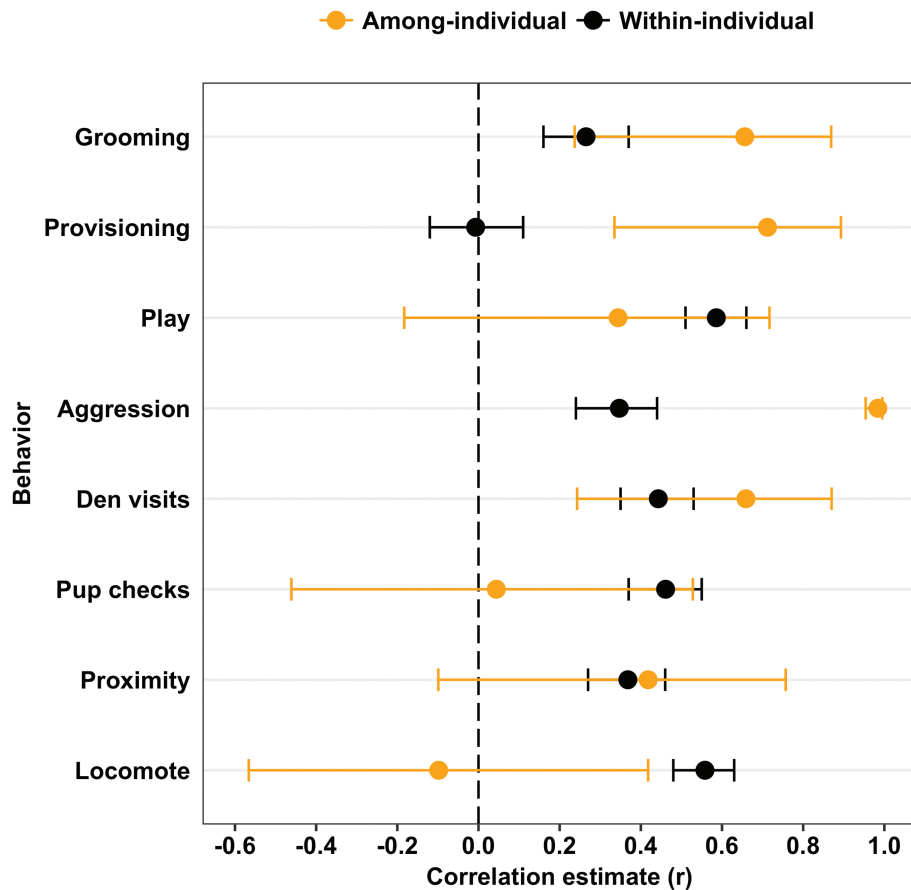


Fig. 2.—Within- and among-individual correlations (r) and 95% CIs among identical maternal and paternal care behaviors (i.e., maternal versus paternal grooming, provisioning, etc.; $n = 16$ individuals, $d.f. = 14$) of coyotes (*Canis latrans*). Correlation values with CIs not containing zero (dashed line) are significant at the $P < 0.05$ level (see Supplementary Data SD4 for specific correlation and covariance estimates, t -values, and P -values).

on milk provided solely by the mother early in life (King et al. 2013). Though mammalian fathers can provision mothers and regurgitate to offspring, the ceiling for paternal investment is much lower than it is for maternal investment. Comparatively, females in avian systems are solely responsible for egg laying, but both sexes have the potential to equally contribute to nest building, nest defense, and provisioning offspring once nestlings hatch (Mutzel et al. 2013; Bebbington and Hatchwell 2015). Sex-specific differences in reproductive costs are thus qualitatively, and perhaps quantitatively, different in mammals and birds, and therefore the ramifications for deviations in paternal care may be more severe.

Do males and females vary in their contribution to care?—When comparing mean-level contributions to care, we found that mothers and fathers only differed in their provisioning rates and proximity during the weaning stage, and later in their initiated play bouts and pup checks during the juvenile stage. Some of these differences are perhaps intuitive. Mammalian mothers provision infants almost exclusively with milk (King et al. 2013). Pups may provide behavioral cues (e.g., muzzled licks, tail wags) to mothers that signal a desire to nurse and may parlay into other behaviors when nursing ceases. For example, during this study, we observed play bouts occurring when females denied nursing bouts during weaning. Nevertheless, the lack of

strong sex differences in the other behaviors observed supports previous literature on the species (Fentress et al. 1987; Asa and Valdespino 1998) and is consistent with examples in biparental rodent and primate systems (Wright 2006; Rafacz et al. 2012; Stockley and Hobson 2016).

Although we controlled for differences in litter size in our analyses, litter size differences within and across mated pairs partially affected parental behavior. Maternal provisioning was greater in the second breeding season, whereas maternal and paternal aggression was also greater for larger litters. Coyotes typically have larger litters with increasing breeding experience (Sacks and Neale 2001; Sacks 2005), and more offspring likely result in greater overall levels of begging. Indeed, Sacks (2005) provides evidence suggesting that litter size is dependent on nutritional condition, which covaries with age. Moreover, Gese et al. (2016) demonstrate that food intake prior to conception is positively related with the number of pups whelped. Coyotes that survive past the yearling stage are more likely to secure home ranges with quality resources (Bekoff and Wells 1982), thus it is biologically plausible that more-experienced breeders would have larger litters. Mechanisms affecting litter size notwithstanding, we found no evidence of change in paternal behaviors from the first to second breeding season (excluding aggression and locomotion), which may hint that mean

Table 5.—Among-individual correlations (r_p) among parental care behavior of coyotes (*Canis latrans*) with 95% CIs (low CI and high CI), partitioned by (a) mothers and (b) fathers. For all behavior, the sample size was 16 individuals ($d.f. = 14$) for both mothers and fathers. Bolded values denote significant correlations after Bonferroni correction for multiple comparisons. See Supplementary Data SD3 for specific correlation and covariance estimates, t -values, and P -values.

	Grooming	Provisioning	Play	Aggression	Den visits	Pup checks	Proximity
(a) Mothers							
Provisioning	0.615 (0.17, 0.85)*						
Play	-0.477 (-0.79, 0.02)	-0.552 (-0.82, -0.08)*					
Aggression	0.909 (0.75, 0.97)***	0.842 (0.59, 0.94)***	-0.585 (-0.84, -0.13)*				
Den visits	0.751 (0.41, 0.91)***	0.719 (0.35, 0.90)***	-0.521 (-0.81, -0.03)*	0.833 (0.58, 0.94)***			
Pup checks	0.544 (0.07, 0.82)*	0.754 (0.41, 0.91)***	-0.512 (-0.80, -0.02)*	0.732 (0.37, 0.90)***	0.751 (0.41, 0.91)***		
Proximity	0.619 (0.18, 0.85)*	0.775 (0.45, 0.92)***	-0.138 (-0.59, -0.38)	0.755 (0.41, 0.91)***	0.545 (0.07, 0.82)*	0.701 (0.31, 0.89)**	
Locomote	-0.512 (-0.80, -0.02)*	-0.411 (-0.75, 0.11)	0.231 (-0.30, 0.65)	-0.504 (-0.80, -0.01)*	-0.601 (-0.84, -0.15)	-0.465 (-0.78, 0.04)	-0.379 (-0.74, 0.14)
(b) Fathers							
Provisioning	0.686 (0.29, 0.88)**						
Play	-0.323 (-0.71, 0.21)	-0.523 (-0.81, -0.04)*					
Aggression	0.734 (0.37, 0.90)**	0.879 (0.68, 0.96)***	-0.632 (-0.86, -0.20)**				
Den visits	0.596 (0.14, 0.84)*	0.787 (0.48, 0.92)***	-0.406 (-0.75, 0.11)	0.856 (0.63, 0.95)***			
Pup checks	0.746 (0.40, 0.91)***	0.531 (0.05, 0.81)*	0.146 (-0.38, 0.60)	0.394 (-0.13, 0.74)	0.413 (-0.10, 0.75)		
Proximity	0.640 (0.21, 0.86)**	0.611 (0.17, 0.85)*	-0.397 (-0.75, 0.11)	0.653 (0.23, 0.87)**	0.641 (0.21, 0.86)**	0.527 (0.04, 0.81)*	
Locomote	-0.297 (-0.69, 0.23)	-0.373 (-0.73, 0.15)	0.237 (-0.29, 0.66)	-0.345 (-0.72, 0.18)	-0.347 (-0.72, 0.18)	-0.240 (-0.66, 0.29)	-0.231 (-0.65, 0.30)

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

contribution to care by fathers is fixed compared with that of mothers.

Does repeatability in care differ by sex?—Mothers and fathers differed in which behaviors were repeatable, deviating from previous literature observing sex-related differences in repeatability estimates. For instance, previous work on house sparrows (*Passer domesticus*—Dor and Lotem 2010) and stitchbirds (*Notiomystis cincta*—Low et al. 2012) indicates repeatability in provisioning efforts does not differ significantly between mothers and fathers. In contrast, studies on long-tailed tits (*Aegithalos caudatus*—MacColl and Hatchwell 2003), savannah sparrows (*Passerculus sandwichensis*—Freeman-Gallant and Rothstein 1999), and house sparrows (Schwagmeyer and Mock 2003; Nakagawa et al. 2007) demonstrate marked differences between sexes in repeatability of provisioning rate, in which males of those species display greater repeatability. Our study is unique in that we estimated repeatability for a series of care behaviors versus only provisioning rate. We did not manipulate available food resources or litter sizes, so it is uncertain how repeatability estimates of mothers or fathers would change with alterations to those parameters. Nonetheless, we suggest that these sex-related differences in repeatable care reflect sex-specific differences in the cost of parental investment.

Do mothers and fathers demonstrate similar within-individual correlations?—Mothers and fathers separately displayed several positive within-individual correlations among the observed care behaviors, the directionality and strength of which was shared across the sexes. For instance, decreases in pup checks corresponded with a reduction in grooming and pup proximity in both sexes, and these 3 behaviors necessitate that parents be near a pup. Interestingly, almost all behaviors except for provisioning demonstrated positive within-individual correlations between mothers and fathers, suggesting that coyote parents may be responsive to changes in parental investment of their partner over developmental time. These data partially support the negotiation model of biparental care initially proposed by McNamara et al. (1999), in which an individual behaviorally adjusts their investment in response to their partner's parental effort (McNamara et al. 1999; Johnstone and Hinde 2006). The model consequently predicts that decreases in parental work rate (i.e., provisioning rates) of the mother should result in compensatory parental effort in the father. Indeed, evidence from great tits (*Parus major*—Hinde 2005), long-tailed tits (Meade et al. 2011; Bebbington and Hatchwell 2015), and burying beetles (*Nicrophorus orbicollis*—Creighton et al. 2014) all demonstrate that parental work rate of fathers increases when their partner's rate is experimentally handicapped. Our study did not intentionally handicap either parent, and it is thus uncertain whether individuals would compensate for deliberate changes in their partner's effort. In addition, several within-individual correlations were not significant after Bonferroni correction. Even so, these preliminary findings are encouraging and provide partial support for the negotiation model in a mammalian system.

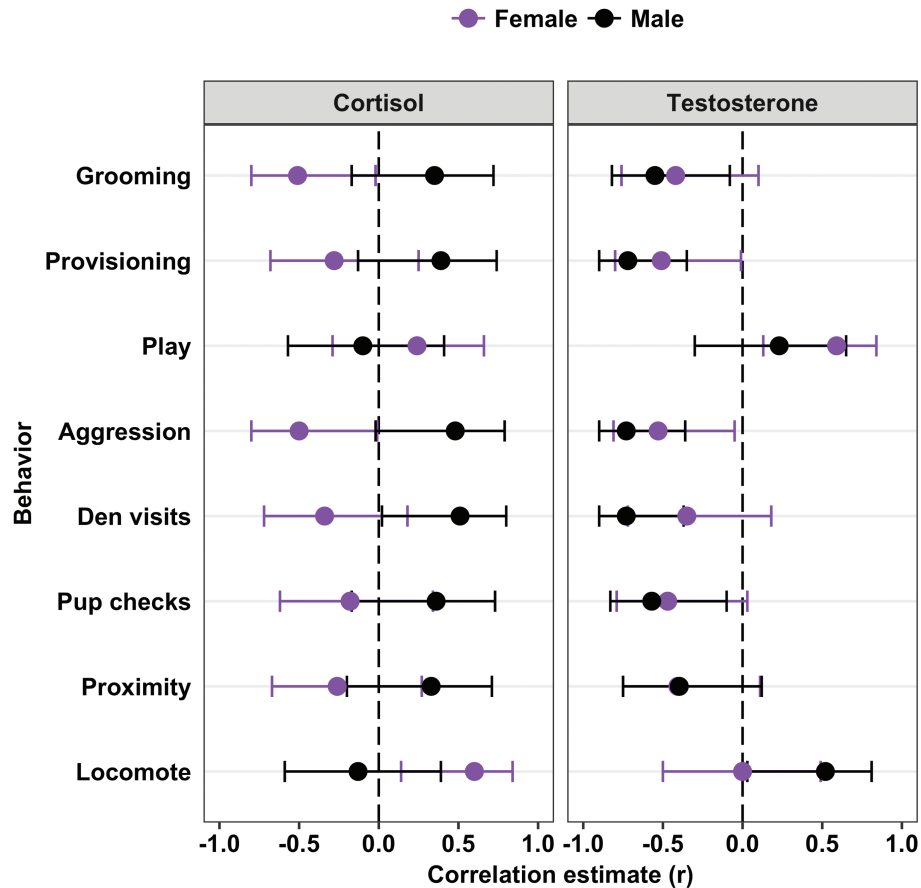


Fig. 3.—Among-individual correlations (r) and 95% CIs describing relationships among best linear unbiased predictor (BLUPs) estimates for parental behaviors of coyotes (*Canis latrans*), fecal glucocorticoid metabolites (i.e., cortisol), and fecal androgen metabolites (i.e., testosterone) during gestation for both mothers and fathers ($n = 16$ individuals, $df = 14$). Correlation values with CIs not containing zero (dashed line) are significant at the $P < 0.05$ level (see Supplementary Data SD5 for specific correlation and covariance estimates, t -values, and P -values).

Do mothers and fathers demonstrate similar among-individual correlations?—Both sexes demonstrated a cadre of among-individual correlations across the 8 observed behaviors, albeit several relationships were not significant after Bonferroni correction. One suite of correlated care behaviors persisted for both sexes: individuals that consistently provisioned offspring more frequently also acted aggressively toward and den-visited offspring more frequently. Similar positive individual correlations exist among nest defense and provisioning in house sparrows (Wetzel and Westneat 2014), and nestling defense and handling aggression in blue tits (*Cyanistes caeruleus*—Fresneau et al. 2014), suggesting that these relationships form parental care syndromes not unlike behavioral syndromes for other personality traits (Sih et al. 2004). However, we may intuitively predict that certain parental behaviors are correlated given their function. In this study for example, when coyote parents checked on pups at den sites, pups responded with submissive gestures that either elicited parental provisioning or aggression with the progression of the weaning stage (C. J. Schell, pers. obs.). Hence, these findings may not appear wholly novel, and given our limited statistical power, it is difficult to determine if parental care syndrome structure is supported in this system.

Is among-individual variation in hormones and care linked?—We provide evidence to suggest that gestational

testosterone—and to a lesser extent, cortisol—are linked with parental care behaviors. Both mothers and fathers exhibited negative among-individual correlations among gestational testosterone, provisioning rates, and pup-directed aggression (Fig. 4), whereas only fathers demonstrated a negative relationship between den visits and aggression (Fig. 3). These data imply that parents, especially fathers, with consistently higher testosterone before parturition display parental personalities that are less attentive. Other biparental mammalian systems have previously shown inverse relationships between circulating androgens and parental care in fathers (Brown 1985; Trainor and Marler 2001; Storey et al. 2006). The novelty here is that individually consistent testosterone profiles observed before the onset of care potentially underscore paternal repeatability. Granted, this assertion assumes that changes in gestational testosterone will result in equivalent changes to parental care, which currently lacks empirical support. Moreover, we suggest further caution, as Hadfield et al. (2010) specifically warn that direct analysis on BLUPs may lead to anti-conservative interpretations due to uncertainty around such estimates; i.e., the P -values reported here are underestimating the actual P -values associated with a correlation coefficient, and the reported CIs are narrower than they would be if uncertainty in BLUPs was incorporated into their estimation.

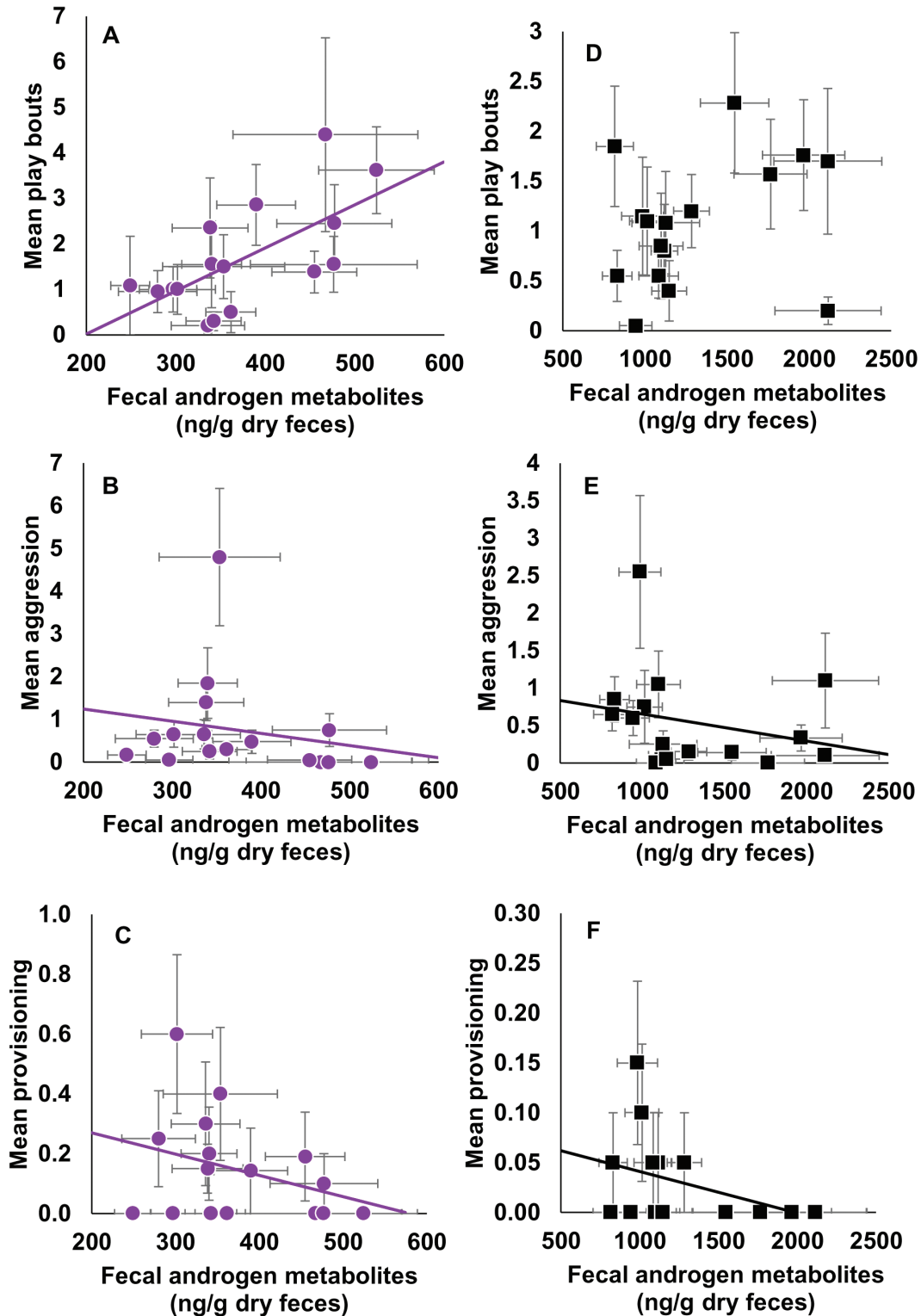


Fig. 4.—Relationships among gestational fecal androgen metabolites (i.e., testosterone, mean \pm SE) and select parenting behaviors (mean \pm SE) of coyotes (*Canis latrans*) for mothers (A–C) and fathers (D–F). Mothers and fathers are presented on different scales, and trend lines indicate statistical significance ($P < 0.05$ level; see Supplementary Data SD5 for full correlation and covariance estimates, t -values, and P -values).

Nevertheless, this study represents an initial step to determining whether preparental variation in physiological traits may predict the level of parental investment made by a parent. Future approaches may be interested in delving into the interplay between testosterone and hormones such as oxytocin

(Gubernick et al. 1995; Kendrick 2000; Graham and Burghardt 2010) and prolactin (Asa and Valdespino 1998; Delahunty et al. 2007; Almond et al. 2008) that have traditionally been associated with increased parental (and mostly paternal) care (Rilling and Young 2014). Ergo, we may predict that parents

with consistently high testosterone have low oxytocin profiles, and thus invest less in parental care.

Conclusion.—Sexual conflict over parental investment is expected to be reduced if paternal investment compensates for maternal work rate in biparental systems (Royle and Smiseth 2012; King et al. 2013). We provide evidence in a biparental canid to suggest that, indeed, fathers contribute equally at the overall mean level of behaviors, as well as adjusting their rate of contribution with changes over developmental time. In addition, among-individual variation in care behaviors corresponded with gestational testosterone, perhaps implying that consistent individual differences in hormonal profiles predict parental type. We statistically categorized repeatability of care behaviors in a mammalian species, as well as decoupled within- and among-individual variances to assess how rate and personality changes are similar between the sexes. Our hope is that this initial effort in the coyote system sparks future research in other biparental mammals to determine how males and females differ in the quality of care provided. For instance, observing parents for 3 or more reproductive cycles would decouple age and experience-related effects to better assess the connection between experience and hormonal correlates. Such research will be foundational in further describing the differences in reproductive costs incurred by mothers and fathers in biparental systems.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Generalized linear mixed model (GLMM) results assessing the effects of parity, development, and the interaction on parenting behaviors.

Supplementary Data SD2.—Within-individual correlation estimates, covariance estimates, 95% confidence intervals, *t*-values, and *P*-values among maternal care and paternal care behaviors of coyotes (*Canis latrans*).

Supplementary Data SD3.—Among-individual correlation estimates, covariance estimates, 95% confidence intervals, *t*-values, and *P*-values among maternal care and paternal care behaviors of coyotes (*Canis latrans*).

Supplementary Data SD4.—Within- and among-individual correlation estimates, covariance estimates, 95% confidence intervals, *t*-values, and *P*-values among identical maternal and paternal care behaviors (i.e. maternal versus paternal grooming, maternal versus paternal provisioning, etc.) of coyotes (*Canis latrans*).

Supplementary Data SD5.—Among-individual correlation estimates, covariance estimates, 95% confidence intervals, *t*-values, and *P*-values among parental behaviors and gestational hormones.

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