Natural History Note

A Free-Ranging, Feral Mare *Equus caballus* Affords Similar Maternal Care to Her Genetic and Adopted Offspring

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abstract: Adoption of nongenetic offspring occurs in a variety of species but is rare in equids. We report a case of adoption by a free-ranging, feral mare *Equus caballus* and compare the maternal care received by her genetic offspring (born 1995) to that of her adopted offspring (born 1996) for the first 30 weeks of development. We compare five measures of care: (1) total time spent suckling, (2) mare aggression during suckling, (3) number of mare-terminated suckling bouts, (4) contact maintenance, and (5) mare-foal distance. For most behaviors, we detected no difference in the mare's treatment of the two foals; however, mare-foal distance was greater for the genetic offspring. We compare hypotheses regarding the reasons for adoption, offering postpartum physiological state as a potential driver.

Keywords: adoption, *Equus caballus*, feral horse, mare, maternal care.

Introduction

Some form of adoption has been reported in more than 120 mammalian species (Riedman 1982), but it occurs rarely. Consequently, very few studies have tracked the progress of adopted offspring in the wild (Gould 2000; Casar and Young 2008), and little is known about the level of maternal care afforded to them and/or their future fitness. More comprehensive descriptions of rare behaviors are necessary if we are to better understand their causes and consequences.

Three cases of adoption in wild/feral equids have been reported in detail; however, of these, none describes a complete, successful adoption in which a female took on the various costs of rearing nonfilial offspring to dispersal (Lloyd and Harper 1980; Penzhorn 1984; Cameron et al. 1999). More recently, adoption was observed in a captive plains zebra *Equus quagga* (Pluháček et al. 2011), but free access to food and water and the overall paucity of natural

conditions may limit what studies of captive animals can tell us about the motivations of their wild counterparts (Calisi and Bentley 2009). Allonursing is similarly rare in wild and feral equids (Penzhorn 1984; Cameron et al. 1999), although it has been recorded in several captive equid species (Pluháček et al. 2012).

Similar hypotheses have been posited to explain why both adoption and allonursing occur in various species (Riedman 1982; Roulin 2002). Misdirected maternal care is thought to occur when females nurse alien offspring inadvertently. This typically occurs in high-density populations in which the benefits of group living outweigh the potential costs, including those associated with nursing alien offspring (McCracken 1984; Boness 1990; Hoogland 2009). The reciprocity hypothesis posits that females attain higher fitness when nursing each other's offspring in a similar fashion than when they do not share nursing (Pusey and Packer 1994). Such females may relieve one another from maternal duties (Perry 1996) and could benefit from each other's varying lactation capabilities (Pusey and Packer 1994) and different immune compounds (Roulin and Heeb 1999). The kin selection hypothesis suggests that mothers will only nurse alien offspring if they share genes by common descent, thereby perpetuating their own genes throughout the population (Packer et al. 1992). This behavior is thought to be more common in species living in social groups composed of closely related females (König et al. 1988). The milk evacuation hypothesis posits that females nurse alien offspring to evacuate a surplus of milk that their own offspring did not consume (Wilkinson 1992). Milk evacuation is thought to occur more often in species such as evening bats *Nycticeius humeralis* and northern elephant seals *Mirounga angustirostris* that need to lose body weight to travel efficiently (Wilkinson 1992; Beck et al. 2000). In addition, in lions *Panthera leo* and warthogs *Phacochoerus africanus*, females with smaller litters engaged in allonursing more frequently, suggesting they had more reserves to share with both genetic and

alien offspring (Pusey and Packer 1994; Plesner et al. 1999). Finally, according to the parenting hypothesis, young females nurse alien offspring to attain additional maternal experience (Roulin 2002).

We examine an instance of adoption in the feral horse *Equus caballus* in which the adopted offspring ultimately was reared to dispersal and achieved reproductive success. We compare the maternal care afforded the adopted offspring versus genetic offspring (of the previous year) for the first 30 weeks of development. Finally, we discuss potential causes for adoption in the context of five measures of maternal care: (1) total time spent suckling, (2) mare aggression during suckling, (3) number of mare-terminated suckling bouts, (4) contact maintenance, and (5) mare-foal distance.

Material and Methods

We studied feral horses on Shackleford Banks, North Carolina, from 1995 through 1997, to determine the effects of variation in the mother-infant relationship. The horses on Shackleford Banks are typical of feral equids, organizing themselves into stable bands of one, two, or three stallions; one to several mares; and their offspring (Rubenstein 1981). The bands are primarily nonterritorial, and animals move within overlapping home ranges (Rubenstein 1981). At the time of the study, approximately 183 animals (~19 individuals/km^2) lived on the island; this was consistent with population densities for the previous 5 years (Rubenstein and Nuñez 2009).

Of the 50 foals observed during the study, one female, heretofore referred to as AF (adopted foal), born in May 1996, was abandoned by her mother, mare 1 (M1), born in 1985. Within 10 days, mare 2 (M2), born in 1980, adopted AF. M2 had lost her genetic foal of that year but had given birth to a female the previous year (GF, genetic foal, born in June 1995, dead in April 1996).

We monitored the mare and each of her two female foals, GF and AF, weekly in 1995 and 1996, respectively. We conducted a total of 130 15-min focal samples (Altmann 1974) over the two foals' first 30 weeks of development (80 focals for GF; 50 focals for AF). We collected data during all times of day (early morning, 0600–0900 hours; late morning, 0900–1200 hours; early afternoon, 1200–1500 hours; late afternoon, 1500–1800 hours). The distribution of focals for each foal is as follows: genetic foal: 5 early morning, 31 late morning, 32 early afternoon, 12 late afternoon; adopted foal: 2 early morning, 11 late morning, 22 early afternoon, 15 late afternoon. Although feral, the horses of Shackleford Banks are habituated to human presence (Nuñez 2000). Regardless, the observer (C. M. V. Nuñez) remained approximately 15 m away from the study subjects to ensure that the animals were not disturbed. The animals did not display significant reactions to observer presence: typically, on observer approach, animals would look at the observer and then continue with their previous activity (C. M. V. Nuñez, personal observation).

We tracked five measures of maternal care: (1) total time spent suckling (suckling bouts/hour × suckling duration), (2) aggression during suckling (including pushes, kicks, bites, and moves away from the foal), (3) number of mare-terminated suckling bouts, (4) contact maintenance (difference in percent approaches and percent departures between mother and infant initiated by the foal; Hinde and Atkinson 1970), and (5) mare-foal distance.

During focal sampling, we recorded mare-foal distance at 5-min intervals and suckling behavior ad lib. (Altmann 1974). We recorded suckling bout length as reported by Cameron et al. (1999). We multiplied suckling rate (number of suckling bouts/hour) by suckling duration as reported by Robertson et al. (1992) to achieve a more comprehensive measure of maternal care (but see fig. A1, available online, for suckling rate data only). We counted the number of horse lengths between individuals and multiplied this measure by 2 to calculate distance in meters (Shackleford horses are ~2 m long). Throughout the study, we randomly measured distances with a measuring tape to ensure the accuracy and consistency of this method.

We assessed M2's physical condition via rump scoring, examining the curvature of the line between the tailbone and the point of the hip. Scores were based on a scale from 1 to 5 (a score of 1 being the poorest; Pollock 1980) and were recorded five times during the study (May and July 1995; April, June, and July 1996). Genetic data were taken from fecal samples of the two mares and the adopted foal but not of potential sires. Relatedness was assessed using 15 microsatellite loci. These data were provided by the National Park Service from a separate study (Conant et al. 2012). We obtained climatology data for the months of January to December in both 1995 and 1996 from the Morehead City WNW Station at 34°44′N; 76°44′W, approximately 8 km from the study site, from the National Climate Data Center (2009).

To assess differences in the care afforded genetic and adopted offspring, we compared generalized linear mixed-effects models of each behavior across the first 30 weeks of foal development with and without random effects of foal identity (variance is nonindependent within an individual) in R, version 2.13.1 (R Development Core Team 2011). We selected best-fit models using Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). For aggression (presence/absence during suckling) and mare termination of suckling, statistical models used binomial error distributions.

All other statistical models used Gaussian error distributions.

Given the limited sample size, we had minimal statistical power to detect possible effects of the ecological environment on maternal care in our models. As such, mean monthly temperature and precipitation (proxies for forage quality) were assessed between years with Wilcoxon signed rank tests in JMP Pro 10 (SAS Institute 1989–2007). Other relevant factors include mare condition; home range size; number, identity, and rank of the stallions present; and band size. These did not differ between years. M2's physical condition was 3.68 ± 0.68 and 3.17 ± 0.27 (mean $\pm$ 1 SE) in 1995 and 1996, respectively. Home range size remained largely constant during the study, measuring 1.12 km^2 and 1.03 km^2 in 1995 and 1996, respectively, with 73% overlap between years. Moreover, the same stallion remained with the band from 1991 until his death sometime in late 1996 or early 1997. The stallion largely retained his rank between years, winning 78.9% and 75% of male-male contests in 1995 and 1996, respectively (Haefele 1996; Gahan 1997). Finally, band size remained constant in both number and demography during the study (6 individuals: 1 stallion, 2 mares, 2 foals, and 1 juvenile).

To determine if M2's behavior differed from other mares, we compared her to three mares of similar age, parity, and ecology that had also reared daughters (table 1). We performed generalized linear models of each behavior by foal age separately for each mare and compared M2's slopes and intercepts to those of other mares, using the Grubbs test for outliers. Analyses were considered significant if $P \leq .05$. All data sets may be accessed via the Dryad Digital Repository: http://dx.doi.org/10.5061 /dryad.4f2t0 (Nuñez et al. 2013).

Results

On May 5, 1996, at 1353 hours, AF was first seen sleeping in the middle of her natal group. She was 1–2 days old. Between 1453 and 1521 hours, the group gradually moved approximately 90 m away. M1 did not attempt to rouse the foal before leaving the area.

When AF woke up at 1622 hours, the group was out of her sight. She whinnied several times but received no reply. At approximately 1640 hours, the foal approached

the group and whinnied. M1 looked up but did not respond vocally. Several other bands were present. AF's lead stallions attempted to retrieve her, but they returned to the group when other stallions approached their females. At 1700 hours, when the observer departed, AF had not rejoined her natal group.

When AF was next seen on May 15, she was suckling from M2. M2 had given birth to a foal between May 5 and May 8; it died between May 8 and May 15. M2 reared AF to 2.08 years of age, at which point AF dispersed. AF gave birth to a colt in 1999 and reared him to dispersal before she was contracepted in January 2000.

Genetic analysis confirmed that M2 was not AF's mother. M1 and M2 share no mitochondrial markers and were sired by different males (Conant et al. 2012). AF's paternity is unknown. She was possibly sired by one of the two males in the band to which M1 belonged for the 5 years before the study.

M2's genetic and adopted offspring did not differ in the total time spent suckling, number of suckling bouts with mare aggression, number of mare-terminated suckling bouts, or contact maintenance with the mare (inclusion of foal identity as a random effect did not improve model fits; see fig. 1A–1D; table 2). M2 was observed in closer proximity to her adopted offspring than her genetic offspring (inclusion of foal identity as a random effect improved model fit; see fig. 1E; table 2).

M2's parental behavior was not different from that of comparable mares (Grubbs test for outliers, all $P > .10$), indicating that her two foals received treatment similar to that of other female offspring. Neither mean monthly temperature (Wilcoxon signed rank, $Z = -0.42$, $P = .60$) nor mean monthly precipitation differed between 1995 and 1996 (Wilcoxon signed rank, $Z = 0.00$, $P = 1.00$).

Discussion

Adoption has been documented in many species (Riedman 1982), but it is rare in equids. We analyze a case of adoption by a free-ranging, feral mare in which the adopted offspring was ultimately reared to dispersal and achieved reproductive success. We compare the early care afforded that foal with that of the mare's genetic offspring of the previous year. To our knowledge, no other study of adop-

Table 1: Mare characteristics at time of study

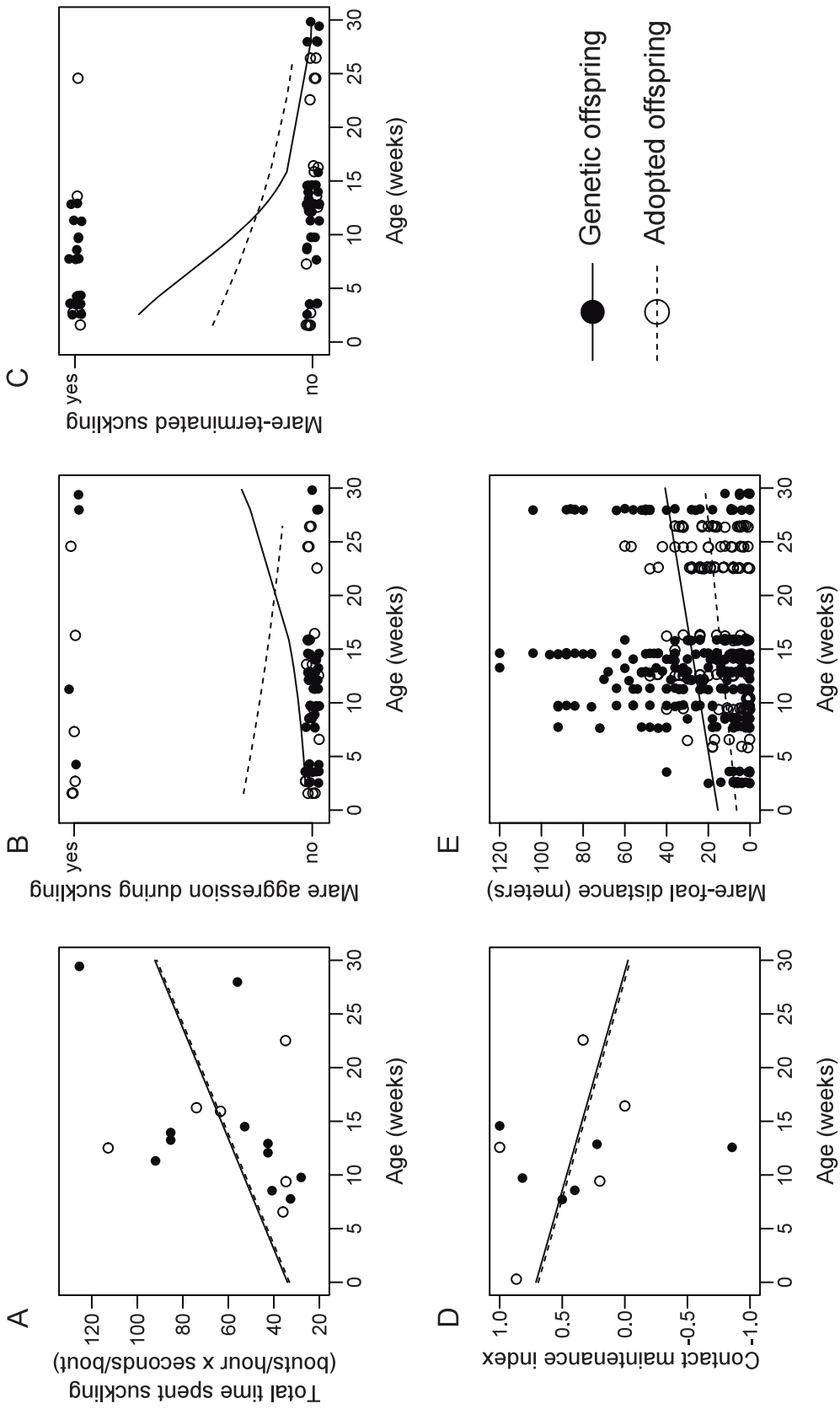| Mare identification	Year born	Mare age (years)	Home range size (km²)	No. foals conceived	No. foals reared to maturity
Mare 1	1985	11	1.00	5	1
Mare 2	1980	16	1.03	6	4
Mare 3	1983	13	1.19	4	1
Mare 4	1986	10	1.03	6	3

Figure 1: Measures of total time spent suckling (*A*), aggression during suckling (*B*), mare-terminated suckling (*C*), contact maintenance (*D*), and mare-foal distance (*E*) for M2 and her genetic (filled circles) and adopted (open circles) offspring.

Table 2: AICc and ΔAICc (from best-fit model, in parentheses) for mixed-effects models of maternal care toward genetic and adopted foals

Behavior	Random slope and intercept	Random intercept only	No random effects	
Intake rate	169.18 (10.59)	161.57 (2.98)	158.58	(.0)*
Mare-terminated suckling	90.96 (4.84)	88.29 (2.17)	86.12	(.0)*
Mare aggression	67.56 (2.70)	66.29 (1.44)	64.85	(.0)*
Contact maintenance	45.02 (14.67)	34.02 (3.67)	30.35	(.0)*
Mare-foal distance	3,741.15 (3.08)	3,738.06 (.0)*	3,764.09	(26.03)

Note: AICc, Akaike's Information Criterion adjusted for small sample size. Asterisks indicate the best-fit model. Best-fit models including random effects indicate that a particular maternal behavior differed between genetic and adopted offspring. Best-fit models without random effects suggest that genetic and adopted offspring were treated similarly. Analyses were considered significant if $P \leq .05$.

tion in free-living equids (Pluháček et al. 2011) describes such a case (Lloyd and Harper 1980; Penzhorn 1984; Cameron et al. 1999). Admittedly, sample sizes are small (as is the case with rare behaviors), so we cannot generalize the results here to the behavior of other mares or females of other species. Our results are unique, however, in that we were able to systematically examine the care afforded the adopted offspring (Blakeslee 1974; Boyd 1980; Waring 2003) and compare it with the care received by the genetic offspring.

With respect to the total time spent suckling, mare aggression during suckling, number of mare-terminated suckling bouts, and contact maintenance, there were no differences. Mare-foal distance did vary, however: M2 and her adopted offspring were observed in closer proximity to one another than were M2 and her genetic offspring. Young foals with closer proximity to their mothers have more access to nutrients and/or protection (Tyler 1972). As foals age, there is a gradual increase in mare-foal distance through approximately the eighth month, after which mare-foal distance tends to remain similar until 1 year of age (Tyler 1972; Nuñez 2000). This increasing independence is thought to facilitate social learning and interaction with other group members (Tyler 1972). The distance between M2 and her two foals did increase with age; however, M2 and her adopted foal were, on average, in closer proximity throughout the foal's first 30 weeks of life. This does not seem to have affected AF's social capacity, however, as she dispersed successfully and reared a colt in 1999 that, after dispersing in 2002, acquired females in 2004; as of February 2013, he was observed with a band of six females (S. Stuska, personal communication, 2000–2010, National Park Service, Cape Lookout National Seashore, North Carolina). Mare-foal distance is one of the few aspects of mother-infant behavior for which the infant has a significant level of control (Tyler 1972; Nuñez 2000). Although contact maintenance did not differ between the two foals (see "Results"), it is possible that the adopted foal's behavior contributed to its closer proximity

to the mare. The foals were reared in similar social and ecological environments; they lived in bands of parallel structure and utilized home ranges and forage of comparable quality. It is unlikely, therefore, that their behavior can be explained by such factors alone.

In feral horses, rearing offspring is often costly for mares because it reduces the likelihood of conception the following year (Kirkpatrick 1995; but see Roelle et al. 2010). On Shackleford Banks, mares that lose their foals are more likely to conceive, either that same season or the next, depending on the timing of foal loss (Rubenstein and Nuñez 2009). The subsequent alleviation of lactation pressure likely makes resources available for the production of additional offspring (Kirkpatrick and Turner 1991). Accordingly, M2 did not conceive in the year immediately following her adoption of AF. So why did M2 adopt? It is unlikely that she misdirected her maternal care. Misdirected maternal behavior occurs when a mother does not recognize that the offspring is not her own and/or the offspring steals her milk. This is made clear on the mother's eventual identification and aggressive rejection of the offspring (Reiter et al. 1978; McCracken and Gustin 1991) and is typically seen in species living in dense groups or in colonies (McCracken 1984; Boness 1990; Hoogland 2009). At the time of the study, Shackleford horses did not live at such high densities. Moreover, population density did not differ from previous years when no adoptions were observed (Rubenstein and Nuñez 2009). Reciprocal nursing was not a driver, as M2 and M1 belonged to different bands and could not benefit from one another's behavior. Moreover, M2 was not inexperienced; she had successfully reared four foals to maturity before the adoption (table 1).

Genetic relatedness to the foal and the need to evacuate excess milk are more difficult to dismiss as potential drivers. As the foal's paternity cannot be definitively confirmed, it is possible that M2 and AF were as closely related as half-sisters, sharing as much as 25% of their genetic material. However, the age differential between them (16

years) makes this scenario unlikely. Moreover, if kin selection were a primary factor in this adoption, we might expect the treatment of offspring to be correlated with relatedness (genetic offspring, $r = 50\%$, vs. alien offspring, $r = 0\%$; Packer et al. 1992). Mares can vary the degree of care they afford their foals (Tyler 1972; Crowell-Davis 1985; Cameron et al. 1999, 2003). For the most part, M2 treated the two foals similarly, suggesting that kin selection was not the primary factor underlying this adoption. Finally, although the loss of her foal likely resulted in a milk surplus (Oftedal et al. 1983), it is unlikely that this remained a driving factor, as M2 continued to nurse AF throughout her first 30 weeks of life and for the 1.5 years following (C. M. V. Nuñez, personal observation).

Another scenario involves M2's postpartum physiological state. In mares and other female ungulates, parturition alters cervical physiology and circulating levels of estrogens and progestins that facilitate mother-infant bonding and maternal care during a critical period (Poindron et al. 1988; Porter et al. 2002; Dwyer 2008). In addition, oxytocin levels peak during fetal expulsion in the mare (Vivrette et al. 2000). Oxytocin has been ascribed several physiological and behavioral effects, including the recognition of pregnancy in the mare (Hansel and Dowd 1986), the olfactory recognition of young in female sheep *Ovis aries* and goats *Capra aegagrus hircus* (Lévy and Keller 2009), and the mediation of maternal behavior in female rats *Rattus norvegicus* (Pedersen et al. 1982). Similarly, prolactin levels increase in the last week of a mare's pregnancy and remain high during early lactation (Worthy et al. 1986). Although its effects on maternal behavior in horses have yet to be studied, prolactin administration stimulates the onset of maternal behavior in female rats (Bridges et al. 1990) and mediates olfactory recognition of pups in female mice (Shingo et al. 2003).

Having recently given birth, M2's hormonal status probably contributed to her willingness and/or ability to adopt after the loss of her own foal. The higher frequency of adoption in domestic mares, for instance, is thought to be an effect of the animals' confinement and the synchronization of parturition (Crowell-Davis and Houpt 1986; Cameron et al. 1999). Conversely, the probability that two such events (the death of one foal and the abandonment of another) will occur in close proximity (in both space and time) probably is lower for free-ranging, feral horses, particularly for those living in temperate climates. For example, at the time of this study, Shackleford mares exhibited a fairly extended birthing period, from March to August, although births did peak in the spring (Nuñez 2000). Such protracted birthing seasons in feral horses (and other equid species; Nuñez et al. 2011) may contribute to the rarity of adoption in the wild (Cameron et al. 1999).

Our results show that successful adoption can occur in feral horses, with equivalent care provided to genetic and adopted offspring. To our knowledge, similar analyses of care to genetic versus adopted offspring have not been reported previously. Although adoption is rare in wild equids, such occurrences are important to document because they offer a more complete understanding of animals' complex and dynamic motivations. Moreover, our study highlights the importance of understanding both individual and species natural history in making reasonable predictions about the causes of behavior in the wild.

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Left, mare 2 and her adopted offspring in 1996. Photograph by C. M. V. Nuñez. *Right*, the adopted offspring as an adult with her second foal in 2009. Photograph courtesy of the National Park Service.