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Original article

Reproduction in North American elk *Cervus elaphus:* paternity of calves sired by males of mixed age classes

John G. Kie, Bruce K. Johnson, James H. Noyes, Christen L. Williams, Brian L. Dick, Olin E. Rhodes, Rosemary J. Stussy & R. Terry Bowyer

Our objective was to examine effects of groups of mixed numbers and ages of male North American elk *Cervus elaphus* on the reproductive performance of females. We conducted research at the Starkey Experimental Forest and Range in northeastern Oregon, USA, during 1993-2000. Each spring in late March, we released 40 female elk, eight yearling (9-month old) male elk and 2-8 branch-antlered elk (i.e. ≥ 2 years of age during rut the following autumn) into a 622-ha fenced pasture. Elk were gathered during autumn and early winter, and were brought to winter feeding grounds where blood samples were drawn to determine pregnancy status. The following spring, females were released into an 80-ha pasture prior to parturition. We searched for and captured newborn calves and obtained ear-punch samples for genetic analysis. We used 18 microsatellite loci to establish paternity of each calf. We varied the ratio of mature males (i.e. ≥ 3 years old) to female ratio from 0.03 to 0.21. As expected, mature males (older and heavier) were more successful in siring calves than were younger males. Within age classes, however, body mass in spring did not accurately predict mating success in autumn. Reproductive rates were not affected by season of grazing by cattle, yearling male to female ratio or mature male to female ratio. Sire age had no effect on mean dates of calf births or on calf weights. Neither sire age nor season of grazing by cattle had significant effects on calf weights; however, mean date of birth was significantly earlier when cattle grazing occurred during the previous autumn than when cattle grazed during the preceding spring. Furthermore, the number of calves sired by yearling males was greater when cattle grazing occurred during autumn, than when grazing occurred during spring. In the years with disruptive cattle grazing during rut, females mated not only with yearling males, in general, but often with those who were lighter in body mass during the previous spring than others in the same cohort. The extent to which those yearling males are untested in combat with older, dominant herd bulls may have genetic consequences leading to differences in fitness and subsequent reductions in calf survival.

Please note that the supplementary information, including Appendix SI mentioned in this article, is available in the online version of this article, which can be viewed at www.wildlifebiology.com

Key words: cattle grazing, Cervus elaphus, conception date, North American elk, paternity, reproduction

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The role of males in reproductive success and population dynamics among polygynous ungulates has gained increased attention among ecologists (Pemberton et al. 1992, Mysterud et al. 2002) and among wildlife managers (Bender & Miller 1999, Noyes et al. 1996, 2002, Biederbeck et al. 2001). For example, with heavy harvest of trophy-class, older male North American elk *Cervus elaphus*, concerns arose regarding the consequences of remaining yearling males doing most of the mating. In particular, the above-mentioned authors hypothesized that yearling males, as less efficient and experienced breeders, would sire fewer offspring, and conception and parturition would occur later and with less synchrony. Later subsequent parturition was thought to provide less time over the summer and autumn to allow calves to gain sufficient weight to survive winter.

North American elk and conspecific Eurasian red deer are polygynous harem breeders, where a large, dominant male attempts to gather, maintain and mate with a group of females while excluding access by subdominant individuals (Geist 1982), although there may be an element of female choice even where dominant males restrict mating opportunities of females (Bowyer et al. 2011). As such, the ability of subordinate males to court females and sire calves is a function of behavioural interactions between sexes (Clutton-Brock et al. 1982). Contrary to the observations by Geist (1982) that females tend to mate only with large males, Squibb (1985) reported that female elk did allow mating by subordinate yearling males, which comprised 21% of 109 observed mounting bouts. In contests among mature stag red deer, "subordinate males… may steal matings during a prolonged fight (between dominant males)" (Krebs & Davies 1978:294).

Previous studies on effects of male to female ratios and sire age on reproductive performance in elk are largely but not invariably in agreement (Mysterud et al. 2002). Most studies reported no effects of older males on conception rates (Noyes et al. 1996, 2002, Bender & Miller 1999, Larkin et al. 2002), although some studies have indicated higher reproductive rates when predominately older males are doing the breeding (Hines et al. 1985, White et al. 2001). Conception and subsequent parturition often is delayed and less synchronous, however, when yearling males are the primary breeders; likely a result of fewer females being bred on their first estrus (Noyes et al. 1996, 2002, Larkin et al. 2002).

In previous research on our study area, we evaluated effects of male age on elk reproduction in an enclosed but wild population of elk, comparing conception dates and pregnancy rates of female elk bred by males of different ages. In a preliminary study, we allowed a single cohort of males to mature from 1½ to 5½ years-of-age and function as principal herd sires (Noyes et al. 1996). Conception dates occurred earlier as male age increased and were significantly different between males $\leq$ 2 years and $\geq$ 3 years-of-age. Rut also became more synchronous when older bulls were the principal sires. Pregnancy rates among females, however, did not differ significantly when male age increased. A second study confirmed these original findings (Noyes et al. 2002). In the two studies, antlered male to female ratios were maintained at $>$ 18:100.

Our objective was to examine effects of groups of mixed aged and numbers of male elk on the reproductive performance of females to determine if there was a minimum mature bull to female ratio needed for early and synchronous mating. We accomplished this using microsatellite DNA analysis of tissue samples taken from males and the subsequent calves they sired in a manner similar to that used by Pemberton et al. (1992) for red deer. Other factors are known or suspected of influencing reproductive performance in elk and red deer such as forage availability, individual body condition, competition with other wild and domestic ungulates, patterns of female aggregation and harem cohesion. In our study, we were able to make some inferences about these potential effects on reproduction.

Material and methods

Study area

We conducted research at the Starkey Experimental Forest and Range in northeastern Oregon, USA (hereafter Starkey; 45°13' N, 118° 31' W). Starkey encompasses 101 km^2 and is managed by the United States Forest Service. Elevations at Starkey range from 1,120 to 1,500 m a.s.l. Vegetation is a mosaic of forest stands and open areas. Common plant associations included Idaho fescue *Festuca idahoensis*, bluebunch wheatgrass *Pseudoroegneria spicata*, ponderosa pine *Pinus ponderosa*, Douglas fir *Pseudotsuga menziesii*, grand fir *Abies grandis* and lodgepole pine *Pinus contorta*. Botanical nomenclature follows United States Department of Agriculture Natural Resources Conservation Service (2011). Campbell Pasture (622 ha), where we conducted our study, was a mix of grasslands and stands of ponderosa pine with two riparian corridors. Annual precipitation averaged 51 cm, and average mean temperatures were 18°C in July and -4°C in January. Further descriptions of the study area are available elsewhere (Rowland et al. 1997).

Starkey supports several species of ungulates including North American elk, mule deer *Odocoileus hemionus* and white-tailed deer *O. virginianus* (Rowland et al. 1997). Predators of elk calves at Starkey include coyotes *Canis latrans*, mountain lions *Puma concolor* and black bears *Ursus americanus*. Starkey is surrounded by a 2.4-m high fence, which prevents immigration and emigration of large herbivores. Elk no longer migrate off the study area to traditional winter ranges because of the fence, and hence animals are kept throughout winter in a holding area and are fed a maintenance diet of alfalfa hay (Rowland et al. 1997, Stewart et al. 2002). In general, elk are held on the winter feeding ground from early December until late March. As a result of the infrastructure at Starkey, the elk population can be manipulated by releasing specific numbers of animals into each study area with a system of fenced alleyways between the winter feeding ground and each of five separate areas on Starkey (i.e. Main Study Area, South Pasture, Campbell Pasture, Northeast-East Pasture, Northeast-West Pasture; Rowland et al. 1997, Stewart et al. 2002).

Approximately 500 cow-calf pairs of domestic cattle are introduced to the main study area around 15 June and removed again by 15 October each year. Cattle graze Starkey on a four-pasture, deferred-rotation system. In odd-numbered years, the order of pasture rotation is: Smith-Bally, Half Moon, Bear (all part of Main Study Area) and Campbell Pasture. In even-number years, the order of rotation is reversed.

Methods

Each spring in late March we marked, weighed and released 40 female elk, eight yearling (9-month old) male elk (which were classified as yearlings during rut that autumn) and 2-8 older, antlered elk (≥ 2 years of age during rut the following autumn) into Campbell Pasture. Loss of individuals each year between spring release and rut in autumn reduced these numbers somewhat (Table 1). Campbell Pasture was grazed by cattle in spring in even-numbered years from about 15 June to 15 July and in autumn in odd-numbered years from about 25 September to 15 October (see Table 1). Campbell Pasture was not large enough to support our study population of elk while being grazed by cattle; hence, we provided supplemental feed for elk from 1 August to 15 September to maintain animal condition relatively constant among years. Supplemental feed was provided at two locations within Campbell Pasture during 1993-1995, and at a single location during 1996-2000.

All elk in Campbell Pasture were gathered during autumn and early winter, and were brought to the winter feeding grounds where blood samples were

Table 1. Year of rut, numbers of elk (females to males 1:2:3:4 years of age and total males) present during rut, males:female ratios and season of grazing by domestic cattle, in Starkey Experimental Forest and Range, Oregon, USA.

Year of rut	♀♀[1]	♂♂ released by age class[1]	♂♂ present during rut[1]	Total males	Total ♂♂:♀♀	Yearling ♂♂:♀♀	Mature ♂♂[2]: ♀♀	Season of grazing
1993	39	8:2:2:0	8:2:2:0	12	0.31	21	0.05	Autumn
1994	-	-	-	-	-	-	-	Spring
1995	40	7:2:2:2	6:1:2:2	11	0.28	0.15	0.10	Autumn
1996	39	8:2:2:0	7:3:2:0	12	0.31	0.18	0.05	Spring
1997	36	8:0:8:0	8:0:8:0	16	0.44	0.22	0.22	Autumn
1998	33	8:2:2:2	8:2:2:1	13	0.39	0.24	0.09	Spring
1999	35	8:1:1:0	6:1:1:0	8	0.23	0.17	0.03	Autumn
2000	38	8:0:8:0	7:0:8:0	15	0.39	0.18	0.21	Spring

[1] Numbers of elk present during rut do not always match the numbers released into Campbell Pasture during spring as a result of mortalities, occasional escapes and one yearling male entering pasture from a surrounding area in 1996.

[2] Mature males defined as ≥ 3 years of age.

drawn to determine pregnancy status (Noyes et al. 1997, Haung et al. 2000). Ear-punch tissue samples were taken from males for genetic parentage analysis. The following spring, females were released into South Pasture (80 ha) prior to parturition. We then searched for newborn calves three times a week from 15 May to 1 July. We captured neonatal calves, estimated their dates of birth, weighed them and obtained ear-punch samples. Calves judged to be < 4 hours old were minimally handled (ear-tagged only) and recaptured on the next search day. We estimated birth mass for all calves aged > 1 day old at capture following Smith & Anderson (1996). Surgical gloves were worn by all persons handling calves, and slings used to weigh calves were washed after each capture. Yarrow *Achillea millifollium*, a pungent native plant, was rubbed on calves after handling to mask human scent.

All capture and handling procedures were in accordance with protocols approved by an established Institutional Animal Care and Use Committee (Wisdom et al. 1993) and were in compliance with guidelines adopted by the American Society of Mammalogists Animal Care and Use Committee (Gannon et al. 2007).

DNA was isolated from ear punches with a standard phenol/chloroform protocol (Sambrook et al. 1989), quantified with a flourimeter (Hoefer) and diluted to 20ng/ul. We selected microsatellite loci for inclusion in our study based on potential variability, amplification efficacy and application in previous studies of elk and related species. Polymerase chain reaction was used to amplify extracted DNA at the following microsatellite loci: BL42, BM203, BM415, BM1009, BM4107, BM4208, BM5004, BM6506, BM848, BM888, BOVIRBP, CeJP15, MAF35, MAF109, RM006 and TGLA334. We selected these bovine and ovine loci based on variability and consistency in scoring. A red deer locus, CeJP15, was also used (J.M. Pemberton, pers. comm.). Details on primer sequences and protocols for microsatellite amplification and allele scoring followed Williams et al. (2002, 2004). Our methods included autoradiography, as described in Williams et al. (2002) as well as automated sequencers (as described in Williams et al. 2004). Because our methods advanced over the number of years we were analyzing samples, our quality assurance focused extensively on enabling the same allele to be identified between methods. So, for consistency in scoring, all detected alleles, as well as molecular weight markers, were electrophoresed on each gel, for each locus.

Paternity of elk calves was assigned using CERVUS (available at: http://www.fieldgenetics.com). This likelihood-based program ranks potential candidate parents from the genetic information provided, identifying a most likely parent. We used genotypes from all individuals to estimate overall allele frequencies, estimates of null alleles and used χ^2 analyses to determine if the frequencies of homozygotes or heterozygotes deviated from expected frequencies.

The methods available in CERVUS have been described in detail elsewhere (Marshall et al. 1998). We conducted simulated parentage analyses using our genotypes, 1,000 cycles and a 1% error rate (which we believe was realistic for our methods). These simulations generate true parental, unrelated parental and offspring genotypes. This allowed us to estimate the resolving power of the suite of loci we used by determining the ability to identify a parent without knowing the genotype of the other parent (total exclusionary power first parent), and to calculate delta, the difference in LOD scores (the sum of the log-likelihood scores at each locus) between the most likely simulated candidate parent and the second most likely.

We analyzed calves for each year with the potential sires from only that year. LOD scores were then calculated for each candidate sire by year and were then ranked. The most likely candidate sire was the one with the most positive LOD score. The difference in LOD scores between the most likely sire and the second most likely sire, delta, was compared against the simulated distributions of delta. We selected 80% and 95% confidence levels, which are typical (Marshall et al. 1998) and useful (Coltman et al. 1999) to assess the deltas of the ranked candidate sires. Because of the likelihood approach, even if mismatches occur between the most likely parent and offspring, an assignment (associated with a confidence level) can still be made.

Results

We observed no deviations from expected allele frequencies, and no evidence of null alleles, at any locus. Based on the simulations, the total exclusionary power for the first parent was 0.948. We were able to assign a most likely sire to every calf. Overall, there were 17 mismatched alleles between calves and their most likely sire. Over all years, 76% of our paternity assignments were at 95% confidence, and all were at or above 80% confidence.

During all years, mature bulls comprised 12-53% of bulls released into Campbell Pasture and sired 57-96% of the 168 calves captured. During all years except 1998, yearling males sired one or more calves (see Supplementary information). There was a positive relationship between sire weight and number of calves sired ($P < 0.01$, $r^2 = 0.41$) across all age classes. There was no relationship, however, between weights of males within age classes during spring and their ability to sire calves that autumn ($P > 0.10$). For example, in 1993, the heaviest yearling (#4186, 128 kg) sired no calves while the lightest yearling (#4192, 101 kg) sired one calf. In 1996, a 3-year-old male (#6458, 196 kg) sired 12 calves while another, heavier 3-year-old male (#6457, 225 kg) sired only five calves. Similar patterns were observed in most other years as well.

Reproductive rates ranged from 0.61 to 0.96 calves/female (Table 2). Reproductive rates were not affected by season of grazing by cattle (spring vs autumn), yearling male to female ratio or mature male to female ratio ($P > 0.10$). Annual male to female ratios for calves averaged 48:52, which did not differ significantly from parity ($P > 0.10$). Neither season of grazing by cattle nor sire age had a significant effect on male to female sex ratios ($P > 0.10$).

Mean Julian date of birth of elk calves was 154.2 days (SD = 10.1 days, N = 163 with available data; see Table 2). Mean date of birth was significantly earlier ($P < 0.01$) when cattle grazing occurred during the previous autumn ($\bar{x} = 151.3$, SD = 7.55 days, N = 96) than when cattle grazed during preceding spring ($\bar{x} = 158.4$, SD = 11.6 days, N = 67). Sire age had no effect on mean dates of calf births ($P > 0.10$). Mean estimated weight of calves at birth (estimated at ages 1-10 days) was 15.15 kg (SD = 2.58 kg, N = 163; see Table 2). Neither season of grazing by cattle nor sire age had a significant effect on calf weights ($P > 0.10$).

Number of calves sired by yearling males showed wide variations among years, averaging 0.60 calves/yearling male when cattle grazing occurred during autumn, and only 0.09 calves/yearling male in years with spring cattle grazing (see Table 2, $P < 0.01$).

Discussion

As expected, males that were older and heavier were more successful, in general, in siring calves than were younger males of lower weight. Within age classes, however, body mass in spring did not accurately predict mating success that autumn. Reproductive rates were not affected by season of grazing by cattle (spring vs autumn), yearling male to female ratio or mature male to female ratio. Sire age had no effect on mean dates of births or weights of calves. Neither season of grazing by cattle nor sire age had significant effects on calf weights; however, mean date of birth was significantly earlier when cattle grazing occurred during the previous autumn than when cattle grazed during the preceding spring. Furthermore, number of calves sired by yearling males was substantially greater when cattle grazing occurred during autumn, than when grazing occurred during spring.

One complication for our study was that grazing by cattle was alternated between spring and autumn,

Table 2. Year of rut, calves captured the following year, reproductive rate (calves/female), mean (SD) calf weight (in kg), mean (SD) calf birth date (Julian) and calves sired by yearling males, in Starkey Experimental Forest and Range, Oregon, USA.

Year of rut	Calves captured ♂♂:♀♀:total	Reproductive rate	$\bar{x}$ (SD) calf birth date	$\bar{x}$ (SD) calf weight	Calves sired by yearling ♂♂	Calves sired/yearling ♂
1993	11:15:26	0.77	151.2 (6.66)	14.36 (1.94)	4	0.5
1994	-	-	-	-	-	-
1995	12:10:22	0.96	146.0 (4.02)	17.04 (1.57)	4	0.67
1996	8:10:18	0.61	161.7 (9.71)	16.09 (2.50)	1	0.14
1997	14:15:29	0.79	156.2 (8.85)	15.59 (3.05)	3	0.38
1998	13:9:22	0.91	167.4 (10.2)	13.79 (2.52)	0	0.00
1999	11:12:23	0.82	150.3 (5.48)	13.73 (2.68)	5	0.83
2000	11:17:28	0.89	149.6 (6.56)	15.02 (1.92)	1	0.14
$\bar{x}$ (SD), autumn grazing[1]		0.84 (0.086)	151.3 (7.55)	15.14 (2.69)		60
$\bar{x}$ (SD), spring grazing[1]		0.80 (0.168)	158.4 (11.6)	14.92 (2.42)		9
$\bar{x}$ (SD), all years		0.82 (0.116)	154.2 (10.1)	15.15 (2.58)		0.38

[1] Season of grazing by domestic cattle (1993, 1995, 1997, 1999 = autumn; 1994, 1996, 1998, 2000 = spring)

which added complexity to our experimental design. This design was fortuitous, however, and resulted in a serendipitous outcome related to our understanding of effects of cattle grazing on rutting behaviour. An additional problem was that the number of elk released into Campbell Pasture did not always correspond to the number of animals present during rut (see Table 1). This was not an obstacle to our investigation, because we confined our analysis to just those elk present.

Consequences of yearling males mating

Interactions between males to settle dominance status during the mating season typically occur through male combat (McCullough 1969, Clutton-Brock et al. 1979, Mysterud et al. 2005). Indeed, older males with large antlers normally mate more often than smaller males (Clutton-Brock et al. 1982, Bowyer 1986), and antler size is related to sperm production and quality (Malo et al. 2005). Furthermore, paternity in polygynous ungulates is strongly skewed toward large males (Maher & Byers 1987, Pemberton et al. 1992).

Among polygynous ungulates, mating by young males, or a low ratio of males to females, holds potential to reduce pregnancy rates, alter timing of births and extend the birthing period. Mating by young, male moose *Alces alces* may reduce rates of pregnancy (Solberg et al. 2002). Timing of births was later when young, male fallow deer *Dama dama* copulated with females (Komers et al. 1999). Conversely, yearling female white-tailed deer gave birth earlier when they copulated with yearling males (Ozoga & Verme 1985). Births are later and less synchronous when younger male elk mate with females (Noyes et al. 1996, 2002). In addition, a low ratio of males to females can reduce the number of young produced for North American elk (White et al. 2001), mule deer (White et al. 2001) and moose (Aitken & Child 1992, Solberg et al. 2002). Timing of births is later as the male to female ratio decreased in reindeer *Rangifer tarandus* (Holand et al. 2003) and moose (Taquet et al. 1999). A lower ratio of males to females, however, did not influence the number of young born in elk (Bender & Miller 1999), bighorn sheep *Ovis canadensis* (Whiting et al. 2008), moose (Laurian et al. 2000, Schwartz et al. 1992) or reindeer (Holand et al. 2003).

Females may mate with small males, however, to avoid the potential risk of delaying estrus until a subsequent cycle. Females must gauge the timing of parturition, such that neonates do not perish from harsh weather conditions in early spring, but are born early enough to have sufficient time to acquire the necessary resources to endure winter (Rachlow & Bowyer 1991, Bowyer et al. 1998). Mating with a small male may be preferable to waiting to mate with a large one. In some instances, late-born young tend to be smaller and have poorer survivorship than early-born neonates (Keech et al. 2000). Research from Starkey, however, has shown that summer nutrition rather than birth date has a much greater effect on body mass at the end of autumn and on subsequent ability of calves to survive harsh winter conditions (Cook et al. 2004).

We hypothesize that we did not observe differences in timing of parturition for female elk in treatments with low numbers of mature males, as did Noyes et al. (1996, 2002), because all treatments contained at least one male ≥ 3 years old. Numerous visual and olfactory cues are available to help females time reproduction, and some of these signals may contain priming pheromones (Whittle et al. 2000). Consequently, some of the deleterious effects noted in other studies may have been offset by the presence of larger males.

Disruption of mating systems

A benefit that may accrue to females of polygynous species during the mating season is a reduction in harassment by young males (Bowyer et al. 2011). Such harassment may have important fitness consequences for females (Real et al. 1996). Four aspects of our study had potential to cause disruption of female aggregations: 1) variation in the male to female ratio, 2) variation in the proportion of young males, 3) changes in the distribution of clumped food, and 4) presence of large numbers of domestic cattle during rut. Neither alterations in the male to female ratio nor in the proportion of young males resulted in marked changes in the number of offspring sired by young males. Cattle grazing, however, positively affected mating by young males in autumn but not during spring. We surmise that cattle*elk interactions during autumn had important influences on the distribution and social cohesion of female groups of elk, and the high density of cattle (500 cow-calf pairs/ 622 ha ~ 1.24 ha/cow-calf pair) may have altered or interfered with harem mating, wherein large males typically sire most offspring.

Elk avoid cattle at Starkey, likely a result of strong interference and exploitive competition between the large herbivores (Coe et al. 2001, Stewart et al. 2002). Cattle are habitat generalists that use level slopes and low elevations compared with elk; both ungulates use areas close to riparian zones (Stewart et al. 2002). At larger spatial scales than in our experiment, elk sought higher elevations when cattle were present (Stewart et al. 2002). The small scale of Campbell Pasture and our experimental units, and the level topography of this area, likely prevented elk from spatially separating themselves from cattle. We suggest that the presence of cattle caused a disruption of female social groups, which provided an opportunity for mating by young males. A harem master would have difficulty in defending widely dispersed and smaller groups of females.

In our study, where all treatments consisted of at least one mature male ≥ 3 years old, proportions of mixed-age males had few discernible effects on reproduction among females. The notable exception was that when grazing by cattle occurred during autumn, not only were yearling males more likely to sire offspring, but paradoxically, mean dates of calf birth were early rather than later as previously reported (Noyes et al. 1996, 2002).

We suggest that parturition was late in years following spring grazing by cattle because elk were placed in a nutritionally restricted environment during summer. Spring grazing by cattle removed $> 40\%$ of herbaceous biomass (J.H. Noyes, Oregon Department of Fish and Wildlife, unpubl. data), and resulted in lower pregnancy rates and delayed conceptions for females (Cook et al. 2004). Elk parturition in years following autumn grazing, however, was not delayed, because females were not subjected to as severe nutritional restrictions prior to rut. Once autumn precipitation commenced, regrowth of herbaceous forage was stimulated and forage quality increased. Consequently, conceptions were earlier with autumn grazing.

In the years with disruptive cattle grazing during rut, females mated not only with yearling males, in general, but often with those that were lighter in body mass during the previous spring than others in the same cohort. Concurrent research on Starkey also has indicated disruption in mating patterns among elk when large numbers of archery hunters were present during rut (Davidson et al. 2012). Such disruptions in social organization and harem cohesion likely lead to greater participation in rut by yearling males. The extent to which the yearling males are untested compared with older, dominant males may have genetic consequences leading to differences in fitness and subsequent reductions in survival of young. More research will be necessary to test these hypotheses.

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