Species resilience in Pleistocene hominids that traveled far and ate widely: An analogy to the wolf-like canids

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Abstract

Morphological and genetic analyses have yet to resolve the question of whether more than one species of Homo existed contemporaneously in the Pleistocene. In an effort to contribute a process-related perspective to hominid phylogenetic reconstruction, this paper uses an analogy to the northern wolf-like canids (the wolves and coyotes) to ask the question, How many Homo species should there be, given their likely behavioral profile(s)? In contrast to earlier comparisons to social carnivores which sought to illuminate specific aspects of hominid behavioral ecology, this paper explores behavioral constraints on the process of speciation itself. The analogy suggests that because Pleistocene Homo probably exhibited high habitat tolerance, they would not have had the opportunity to speciate, especially in Africa. In contrast to an earlier single-species hypothesis based on competitive exclusion between sympatric hominid species, this paper explores constraints on the process of speciation under conditions of temporary allopatry.

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Introduction

The demonstration that two extremely divergent hominid species overlapped temporally in East Africa during the Early Pleistocene laid to rest the single-species hypothesis of hominid evolution (Leakey and Walker, 1976). But it has proved difficult to demonstrate unequivocally that additional cladogenic events have occurred in the genus Homo. Therefore, a fundamental question in paleoanthropology—whether more than one species of Homo ever existed contemporaneously in the Pleistocene—has defied consensus (e.g., compare “splitters”—Groves, 1991; Schwartz and Tattersall, 1996; Klein, 1999; with “ lumpers”—Henneberg and Thackeray, 1995; Wolpoff, 1999; Cunroe and Thorne, 2003).

Neither morphological nor genetic data have resolved the phylogeny of Pleistocene Homo. This is in large part because the taxonomic significance of morphological and genetic differences between closely related animals is often unclear (Tattersall, 1986, 1993; Jolly, 1993; Mayr, 2000; Ahern et al., 2005). Among extant animals, for example, “good” species can be nearly indistinguishable morphologically (cryptic species), yet intraspecific variation can also be so great that subspecies would be mistakenly identified as species in the absence of behavioral information (e.g., in baboons: Jolly, 1993). Likewise, seemingly decisive analyses of modern human (beginning with Cann et al., 1987; reviewed in Relethford, 2001) and fossil hominid DNA (Krings et al., 1997, 2000), interpreted to support a recent African origin of anatomically modern humans, continue to be challenged on both methodological and interpretive grounds (e.g., Relethford and Harpending, 1994, 1995; Hawks et al., 2000; Adcock et al., 2001; Relethford, 2001; Templeton, 2002; Eswaran et al., 2005).

Information pertaining to higher-order processes and speciation mechanisms can be recruited to help evaluate phylogenetic hypotheses (Foley, 1991; Turner and Wood, 1993; Conroy, 2002). For example, data relevant to the behavioral potential for population isolation in the Pleistocene bear...
directly on phylogenetic hypotheses, since speciation depends on reproductive isolation. Relatively little attention has been devoted to exploring this issue (but see Foley, 1984, 1989; Turner, 1984; Gollop and Foley, 2002; the issue has received more attention for the Mio-Pliocene, e.g., Vrba, 1985, 1995; Bromage and Schrenk, 1999; Kingdon, 2003), yet a compelling phylogenetic reconstruction should address the following questions: What conditions could have led to sustained geographic vicariance,1 and subsequent reproductive isolation, of a given hominid population? Where could this have occurred? What behavioral conditions would have made genetic divergence likely, or unlikely, in an isolated population?

Comparisons to adaptively similar modern species may suggest answers to these questions. In this paper, I use an analogy to the wolf-like canids (Canis lupus, C. rufus, and C. latrans) to ask the question, How many Homo species should there be, given their likely behavioral profile(s)? (cf. Foley, 1991). The wolf-like canids are behaviorally similar to Pleistocene hominids in three key ways: (1) they are adapted for endurance locomotion, (2) they have a diverse diet, and (3) they are socially flexible. These characteristics lead to high habitat tolerance, which appears to have made the wolf-like canids resistant to allopatric speciation. I argue that analogous habitat tolerance would have likewise made isolation and allopatric speciation among Pleistocene Homo unlikely, especially in Africa. In contrast to an earlier single-species hypothesis which posited competitive exclusion between sympatric hominid species (Wolpoff, 1971), this paper explores behavioral constraints on the process of speciation itself under conditions of temporary allopatry.

Primate analogies and their limitations

Although debate persists concerning the nature of biological species and how to define them (Claridge et al., 1997; Wheeler and Meier, 2000; summarized in Groves, 2001), most theorists agree that some degree of allopatric isolation is essential to speciation (following Mayr, 1963; and including vicariance, peripatric, and parapatric models: Futuyma, 2005). Sympatric or stasipatric speciation mechanisms (cf. Groves, 1991) are more difficult to model and less commonly invoked (Vrba, 1995; Turner, 1999; Futuyma, 2005). Ideally, hypotheses about speciation should include proposals concerning population isolation, genetic divergence, and recontact. But this is not easily achieved for extinct populations known from small samples of fossils. For these “morphospecies,” crucial biogeographic information regarding ecotones, geographic barriers, and range boundaries is difficult to obtain (Grubb, 1999), and taxonomic decisions rely primarily on quantifying morphological and genetic differences within and between fossil samples (e.g., Schillaci and Froehlich, 2001; Harvati et al., 2004).

Efforts to model hominid reproductive isolation have focused on the use of extant primate species as analogs, with the choice of an analog species depending on its phylogenetic and ecological profile (Jolly, 1993, 2001; Holliday, 2003). Jolly (2001) cites two criteria in support of his preference for baboons over apes as analogs for hominids, beyond the fact that their relative phylogenetic distance will help avoid the error of mistaking parallelism for homology. First, he argues that the best models for thinking about hominid taxonomy will be clusters of minimally differentiated species that have experienced recent radiations (2001: 180). Second, species that are ecological generalists are preferred (2001: 195), presumably because ecological flexibility will permit a wide geographic distribution within which allopatra can be established.

But while baboons may constitute a good primate species cluster for modeling hominid population dynamics, the baboon analogy nonetheless contains two important shortcomings. First, the preference for a species that has manifested a recent radiation into distinct allotaxa restricts us to imagining that Pleistocene Homo were distributed as allotaxa in a way similar to that now found among baboons, which exhibit relative geographic isolation and narrow hybrid zones. However, for reasons discussed below, Pleistocene Homo may not have been divided along ecotones as baboons and many other primate species are today. Second, although baboons are ecologically flexible compared with many other primates, they may nonetheless be relatively specialized compared to hominids. This possibility stems from the proposition that hominids, at least by the emergence of Homo around 2 mya, were radically different ecologically from any known primate (Potts, 1994; Milton, 1999).

The unusual (for a primate) nature of hominid behavioral ecology

At least three lines of evidence imply that hominids were dramatically different from other primates ecologically. First, at least by the Pleistocene, bipedality appears to have represented an adaptation to walk and run farther and more efficiently than other primates can (Rodman and McHenry, 1980; Haesler and McHenry, 2004; Bramble and Lieberman, 2004). Despite the long-running debate regarding the relative efficiency of australopithcine bipedalism (Taylor and Rowntree, 1973; Rodman and McHenry, 1980; Wolpoff, 1983; Jungers and Stern, 1983; Lovejoy, 1988; Steudel, 1995; Richmond et al., 2001), the postcranial morphology of Pleistocene Homo was certainly more like that of modern humans (Brown et al., 1985), and increases in both limb length and body mass imply reduced costs of locomotion (energy/unit time) and transport (energy/unit distance) (Taylor et al., 1970; Steudel, 1995; Leonard and Robertson, 1997a). Improved locomotor efficiency, in turn, would have offered new foraging opportunities (Carrier, 1984), and was probably accompanied by significant increases in range size and

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1 Following the usage in Vrba (1995), I use the term “vicariance” to refer to fragmentation in the geographic distribution of a species that, if sustained, can result in speciation. Bromage and Schrenk (1999: glossary) credit Grubb (1999) with a usage of vicariance, not adopted here, which appears essentially synonymous with the term “allopatric speciation.”
reproductive dispersal potential (Foley, 1992; McHenry, 1994; Leonard and Robertson, 1997a, 2000; Foley and Elton, 1998; Antón et al., 2002).

Second, by the emergence of Homo roughly 2 mya, hominin dietary breadth must have increased in response to the substantially higher energetic demands of relatively large brains (Shipman and Walker, 1989; McHenry, 1994; Aiello and Wheeler, 1995; Leonard and Robertson, 1997b; Ungar et al., 2006). Higher nutritional requirements would have demanded a novel ecological solution(s) to access more easily digested, higher-calorie foods. Two possible strategies, not necessarily mutually exclusive, would have been an increase in meat consumption by hunting (Washburn and Lancaster, 1968; Carrier, 1984; and many others) and/or scavenging (Schaller and Lowther, 1969; Blumenschine, 1987; Domínguez-Rodrigo, 1999), and cooking (Wrangham et al., 1999). In both cases, greater dietary breadth is implied. Increased meat consumption does not eliminate plant-based nutrition, but rather would be expected to supplement it, and perhaps even require the addition of new plant products (Cachel, 1997). In the case of cooking, which may date to the early Pleistocene (Wrangham et al., 1999; but see Brace, 1997), many more plant foods would become available because high heat breaks down otherwise indigestible hard fibers and can neutralize plant toxins (Leopold and Ardrey, 1972). Increased dietary breadth, in turn, would make new ecological communities accessible to hominids, eliminating at least some barriers to individual ranging and dispersal (Potts, 1994).

Third, with increasingly larger brains, Pleistocene Homo were likely to have been increasingly emancipated from modal forms of social organization. That is, we should expect that they were even more behaviorally flexible than other primates, and therefore less likely to be constrained by ecological barriers, and more likely to be ecologically heterogeneous. Although most nonhuman primate species can be characterized by a modal form of social organization (e.g., organized in monogamous, one-male/multifemale, or multimale/multifemale groups), it is clear that they manifest tremendous intraspecific variability in behavior and social organization associated with ecological variability (Fuentes, 1999; Arcadi, in prep). With increased relative brain size, Pleistocene Homo were possibly even more socially labile, perhaps more easily altering their social behavior and organization, both within and between groups, to meet novel ecological demands (Foley and Lee, 1989; Rodseth et al., 1991).

Taken together, these behavioral characteristics suggest that all Pleistocene Homo had the potential to utilize a wide range of food resources found in varying abundance, and could travel far to obtain them, as compared with other primates. There is every reason to suppose, and some geological and archaeological data to support the idea, that Pleistocene Homo exhibited high habitat tolerance (Kingston et al., 1994; Potts, 1994). Cultural developments such as the evolution of linguistic capacities, increasingly sophisticated tool technologies, the controlled use of fire, clothing, and shelter would have continued to increase habitat tolerance in Middle and Upper Paleolithic hominids (i.e., access to higher latitudes and altitudes: Turner, 1984).

These considerations lead us to question the applicability of primate models for understanding hominin population dynamics, because the potential for genetic differentiation in geographically separate populations would have been dramatically reduced in hominids compared with other primates, despite their vast geographic range. This is because dispersing populations would have relied on behavioral flexibility, and not genetic differentiation, to succeed in colonizing new environments, as the following examination of speciation theory shows.

Implications of habitat tolerance for the establishment of allotaxa

The allopatric speciation model (see references above) stipulates that speciation results when gene flow between populations is diminished or interrupted, and founder effect and/or selection result in the evolution of pre- and post-mating isolating mechanisms. However, continued divergence and speciation are not an inevitable consequence of allopatry, and requisite degrees of genetic and morphological divergence are quite variable (Mayr, 1963, 2000). Thus, geographic separation is not a sufficient condition for speciation (Vrba, 1999). A substantial body of empirical evidence shows that species cohesion can be maintained under conditions of allopatry, sometimes for very long periods of time (e.g., several million years in the polytypic salamanders, *Ensatina eschscholtzii*; Moritz et al., 1992; Wake, 1997). In some cases, allopatric populations can manifest minimal geographic variation in spite of dramatically different ecological circumstances (e.g., *Tanysiptera galatea*; Mayr, 1992). Thus, while selection can produce morphological differences between separated populations of a magnitude sometimes observed between species, even limited gene flow can sustain polytypy without speciation (reviewed in Rice and Hostert, 1993). For speciation to occur, conditions must prevail that promote genetic divergence between founder and parent populations, and this divergence must be either directly or indirectly linked to specific mate recognition systems (Paterson, 1985).

Vrba (1980: 73—80, 1995: 30—31; see also Eldredge, 1979: 14) has argued that the likelihood of speciation depends on the degree to which a species is environmentally specialized (the “effect hypothesis”). This hypothesis assumes that dispersal is an inevitable and constant feature of animal populations (see also Corbet, 1997; Grubb, 1999). Based on an analysis of species richness in terrestrial mammals, she found that ecologically specialized taxa tend to be more speciose than environmental generalists. The theoretical explanation for this
finding is that narrow habitat specialization ("stenotopy") precludes easy colonization of new ecological communities, so that peripheral population isolates will survive only rarely, and only if they differ genetically from their parent stock. By contrast, peripheral populations of species characterized as environmental generalists ("eurytopy"), by being more behaviorally flexible, can more readily colonize diverse habitats without the necessity of differing genetically from their parent stock. Thus, dispersal will more often result in population fragmentation in a stenotopic species because the failure to persist in most new ecological settings will produce gaps in the species' distribution. Likewise, climate-driven ecological disruptions are more likely to fragment stenotopic than eurytopic populations. Thus, eurytopes are more likely to maintain population continuity during range expansion, even as they colonize new ecological communities.

Analyses of comparative species richness in a range of mammalian taxa provide support for the effect hypothesis. The Alcelaphini (blesbuck, hartebeest, wildebeest), specialized consumers of bulk and roughage, exhibited a radiation of 27 species over the past six million years, whereas the Aepycerotini (impalas), adaptable ruminants that can adjust the structural components of their stomachs in response to diet (Hofmann, 1973: 235), evolved only 1 or 2 species during the same period (Vrba, 1980). Similarly, the forest-adapted guenons (Cercopithecus spp.) evolved 18–25 species over the last 0.5–1.0 million years (Groves, 2001; Butynski, 2002), whereas the more omnivorous and habitat tolerant booons (Papio) generated between 1 and 5 species during this same period (Jolly, 1993; Groves, 2001). Taking high mobility into consideration, stenotopic horses (e.g., Equus, 1991; lions, Panthera leo; Turner, 1990) did not. Vrba (1980) proposed that, in general, we would expect carnivores to be relatively eurytopic compared with herbivores, since the former tend not to be prey-species-specific (they tend to be prey-size-specific), whereas the latter may less readily adjust to new vegetation types.

Because Pleistocene hominids were likely to have been environmental generalists that traveled far in search of diverse resources, the effect hypothesis suggests that they would not have evolved many, if any, allo taxa across their impressive geographic range (cf. Grubb et al., 1999). This conclusion is at odds with recent assessments of both Early and Late Pleistocene hominid taxonomy that identify multiple contemporaneous Homo species distributed across continuous terrestrial habitat (e.g., Schwartz and Tattersall, 1996; Wood and Collard, 1999). However, its theoretical feasibility can be evaluated by asking whether it is possible for a large, eurytopic mammal species to be extremely widely distributed (i.e., more than one continent) and show statistically significant regional variation in morphology, yet resist speciation, as evinced by minimal genetic differentiation. More particularly, are there modern species that meet these criteria, while at the same time being behaviorally and ecologically similar enough to what we think hominids were like to support a compelling analogy (e.g., more intuitively satisfying than one based on rodent species: Wolpoff et al., 1984: 447)?

A non-primate analogy for Pleistocene hominids: wolves and coyotes

Because of their high habitat tolerance, social members of the order Carnivora are good candidates for modeling behavioral aspects of hominid biogeography (Schaller and Lowther, 1969). Of these, the northern hemisphere wolf-like canids (gray wolf, Canis lupus; red wolf, C. rufus; coyote, C. latrans) are especially intriguing because of their exceptionally wide distribution, variable morphology, and adaptive similarity to Homo. In contrast to previous carnivore and primate analogies, which have mainly focused on the behavioral ecology of carnivory and possible interspecific interactions among Plio-Pleistocene hominids (Schaller and Lowther, 1969; Cachel, 1975; Thompson, 1975; Hall, 1977, 1978; Du Brul, 1977; Stevenson, 1978; Foley, 1984, 1992; Turner, 1984; Leonard and Robertson, 1992, 1997b, 2000; Foley and Elton, 1998; Sikes, 1999; Simmons, 1999; Holiday, 2003), the goal of this comparison is to gain insight into the likelihood of allo-taxic evolution in later hominids.

Endurance locomotion, dietary breadth, and social flexibility in the wolf-like canids

Endurance locomotion. Wolves and coyotes are cursorial carnivores that typically capture their prey after prolonged chases [compared with an ambush from concealment, as in leopards (Panthera pardus), or a swift rush, as in cheetahs (Acinonyx jubatus)]. Wolves can sustain trotting speeds of 8–9 km/hr for several hours (Mech, 1994: Table 1) and can maintain running speeds of 55–70 km/hr for 20 minutes or more (Nowak, 1991). Predation chases usually cover less than 5 km, but can be much longer: a record pursuit of 20.8 km was observed by Mech and Korb (1978). Daily travel distances range from a few to 200 km (Mech, 1970), with typical averages of 20–30 km/d (e.g., Mech, 1970: 160; Pulliainen, 1975: 298; Ciucci et al., 1997: 811; Jedrzejewski et al., 2001: Table 1). Dispersal distances are also variable, from a few kilometers to take over a territory adjacent to an individual’s natal range (e.g., Mech, 1987: 65; Gese and Mech, 1991: 2949), to average distances of a few hundred km (e.g., Boyd et al., 1995: Table 1; Wabakken et al., 2001: 721), to directional movements of up to record observations of 840 km for a Rocky Mountain female (Boyd et al., 1995: 139) and 886 km for a Minnesota male (Fritts, 1983: 166).
Recorded territory sizes range from 33 km² (L.D. Mech and S. Tracy, unpublished data, in Mech and Boitani, 2003a: 21) to 4335 km² (Mech et al., 1998: Table 2.5); for packs following caribou migrations, ranges can swell to 63,058 km² (Walton et al., 2001: Table 1). It is also noteworthy that wolves are competent swimmers, with a record distance of 13 km observed by P.C. Paquet (pers. comm. in Mech and Boitani, 2003b: xv).

**Dietary breadth.** Wolves and coyotes usually rely on mammalian meat, but they are both known to fish (Gier, 1975: 250; Mech et al., 1998), to eat birds, lizards, crustaceans, and insects (Young and Goldman, 1944: 211; Gier, 1975: 250), and to consume some types of plant matter in large quantities when available (e.g., fruits and grass: for wolves, see Peterson and Ciucci, 2003; for coyotes, see Niebauer and Rongstad, 1975; McManah, 1978; Wade, 1978; Knowlton and Stoddart, 1992). Variability in prey size selection, though common in carnivores, is extreme in wolves and coyotes. In most areas, wolves concentrate on medium-to-large-sized (i.e., up to 1000 kg) ungulates. Nonetheless, wolves can effectively hunt and subsist on much smaller prey, including hares (Lepus americanus), beaver (Castor spp.), and some small rodents (reviewed in Mech and Peterson, 2003; Peterson and Ciucci, 2003). Conversely, coyotes, which are roughly half the size of wolves, usually rely on small rodents, rabbits, and fruits, but will take prey as large as deer when these are available (reviewed in Boer, 1992). In both species, wide dietary breadth is reflected in their generalized craniodental morphology compared with other carnivores (reviewed in Biknevicius and Van Valkenburgh, 1996; Peterson and Ciucci, 2003).

Flexibility in prey size selection in the wolf-like canids is the result of two factors, one morphological and one behavioral. First, though relatively large, these predators are sufficiently small to subsist on smaller prey when necessary (by contrast, the extinction of dire wolves, *Canis dirus*, may have resulted in the extinction of *C. dirus*, beaver (Castor spp.), and some small rodents (reviewed in Mech and Peterson, 2003; Peterson and Ciucci, 2003). Conversely, coyotes, which are roughly half the size of wolves, usually rely on small rodents, rabbits, and fruits, but will take prey as large as deer when these are available (reviewed in Boer, 1992). In both species, wide dietary breadth is reflected in their generalized craniodental morphology compared with other carnivores (reviewed in Biknevicius and Van Valkenburgh, 1996; Peterson and Ciucci, 2003).

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**Social flexibility.** While they are not alone among the carnivores in demonstrating complex social dynamics, wolves and coyotes nonetheless display interesting parallels to extant primates, and thus perhaps to hominid primates, in their social flexibility. In particular, these canids exhibit a surprisingly wide range of group compositions. Mated pairs with offspring appear to be the most common type of social group, but other arrangements are frequently observed. For example, the following kinds of groups have now been documented among wolves: one male/one female; one male/adult son/one female; one male/two females; all male groups; and large, fusion groups containing multiple adult males and females (reviewed in Mech and Boitani, 2003a). Both sexes disperse and both sexes are capable of joining existing, unrelated breeding groups (Lehman et al., 1992), despite the risk of lethal aggression (Mech and Boitani, 2003a). Average pack sizes are typically between 5 and 10 individuals in North America, and maximum pack sizes of over 20 individuals are not uncommon (Fuller et al., 2003: Table 6.1). Similarly, although maximum observed group sizes are lower for coyotes than for wolves, they too are flexible. While most coyote studies have reported the prevalence of mated pairs and offspring, groups as large as 22 individuals have been observed when large prey are available either for capture or as carrion (Camenzind, 1978; Brundige, 1993 and Sabean, 1993 in Patterson and Messier, 2001: 463; Patterson and Messier, 2001).

**Habitat tolerance, polytypy, and genetic differentiation in the wolf-like canids**

In general, meat-eating carnivores tend to be eurytopic (Vrba, 1980), reflecting the fact that from the point of view of digestion, animals are a more consistent and predictable nutritional resource than plants, which boast a myriad of physical and chemical defenses and vary greatly in nutritional value. While prey animals from different ecological communities may demand different capture strategies, they are unlikely to demand particularly different processing techniques or digestive requirements once acquired. Large and small animals may be consumed in slightly different ways (Blumenschine, 1987), but meat and bone themselves, unlike plant products, are comparatively uniform across species and environments, so that processing varies little within prey size classes (Van Valkenburgh, 1989; Biknevicius and Van Valkenburgh, 1996).

As a consequence of their habitat tolerance, carnivores can occupy vast geographic ranges, encompassing many ecological communities, while exhibiting comparatively low species diversity. The canids exemplify this pattern. The family Canidae includes 16 genera and 36 species, which are distributed throughout four continents, excluding the dingo in Australia which is descended from the domestic dog. By comparison, the Cercopithecidae comprises 21 genera and roughly 125 species distributed across primarily tropical and subtropical Africa and Asia (Nowak, 1991; Groves, 2001). Wolves and coyotes in particular occupy extensive geographic ranges and are capable of rapid colonization. Wolves remain second only to humans in extent of geographic distribution and, presumably, habitat tolerance (Boitani, 2003). In the wake of the extirpation of the wolf from most of its North American range, coyotes succeeded in colonizing most of that continent in less than 100 years. Both species can thrive in seemingly any habitat—deserts, wetlands, northern forests and tundra, and all manner of agricultural, suburban, and urban habitats
in between (Moore and Parker, 1992; Fritts et al., 2003). Both wolves and coyotes are largely unhindered by environmental heterogeneity: they can subsist on a wide variety of foods, tolerate extreme temperature variation (−21°C to +48°C for wolves: Mech and Botani, 2003b: xv), sustain high levels of physical exertion for extended periods of time, and adjust group size and composition to prey biomass and prey size, all of which have the effect of increasing the range of exploit-able ecological communities available to them.

As one might expect in a widely distributed species, consid-erable morphological variation exists across the range of mod-
er C. lupus. The biggest animals are found in the northern populations of North America and Eurasia (e.g., mean body weights for male and female C. l. occidentalis are as high as 47.0 and 40.0 kg, respectively: Mech et al., 1998, n = 18 and 15, SD not provided; for Eurasian C. l. communis, mean weights are 44.7 ± 3.0 and 34.2 ± 4.2 kg, respectively: Wabakken et al., 2001, n = 15 and 7). The arctic subspecies (C. l. arctos in North America, C. l. albus in Eurasia) are slightly smaller, with the North American C. l. arctos being distinguished by the rela-tively largest carnassials of any population. Medium sized wolves are found in wide bands across the intermediate latitudes of North America (C. l. nubilis) and Eurasia (C. l. lupus). The smallest wolves are found in southern localities: C. l. lycaon, the smallest C. lupus subspecies in eastern North America, in southeastern Canada; C. l. baileyi in Mexico; and C. l. pallipes in south Asia and the Arabian peninsula. Mean body weight values for some of these populations are less than half those of their northern conspecifics (e.g., 20.1 and 17.0 kg for male and female C. l. pallipes: Mendelsohn, 1982, n = 7 and 6, SD not provided). Body weights of C. rufus, which were distributed historically in southeastern North America, are at the low end of the North American wolf range (e.g., 22.7 ± 3.9 and 20.0 ± 2.7 kg for males and females: Riley and McBride, 1975, n = 26 and 26). Canis latrans body weights historically fell below the ranges of North American wolves (e.g., 15.0 ± 2.0 and 13.2 ± 1.8 kg for males and females: Riley and McBride, 1975, n = 15 and 17); C. latrans populations that have colonized the Northeast over the last 50 years (Hilton, 1978) are larger, overlapping the lower end of the body weight range of neighboring C. lupus (20.3 and 18.0 kg for males and females: Silver and Silver, 1969, n = 8 and 6, SD not provided). Cranial dimensions can also vary greatly between wolf subspecies, with the most distinctive wolf populations found at the peripheries of the species range (Nowak, 2003: 247).

However, although sufficient regional differences in body size and cranial metrics exist to designate some 10 subspecies of modern C. lupus (Nowak, 1995, 2003), all workers agree that clines and substantial metric overlap characterize regional variation in wolves (reviewed in Brewster and Fritts, 1995). Pelage color has proved too variable to be of taxonomic value, with the single—but not invariable—trend being a north-south color cline among northern populations from lighter to darker (Gipson et al., 2002). Thus, while there is some debate about the identities and boundaries of subspecies (usually in the con-text of conservation policy), all analyses point to the existence of only one or two (i.e., if C. rufus is distinct from C. lupus) species distributed across a geographic range that spans three continents. Clinal variation and metric overlap reflect the existence of extensive gene flow throughout the species range resulting from large territories and high dispersal distances (Nowak, 2003). Moreover, despite regional variation in mor-phology, general behavioral similarity prevails among all wolf populations.

The emergent profile of modern wolves is that of a widely distributed, polytypic species for which subspecific designa-tions may be useful hypotheses for reconstructing biogeographic history, but represent little or nothing about differences in behavioral ecology or specific mate recognition systems between populations (Mech, 1991: 315).

Molecular genetic analyses of C. lupus interpopulation vari-ability (reviewed in Wayne and Vila, 2003) are consistent with this interpretation. Studies employing allozyme electrophoresis, mitochondrial (mt) DNA restriction site analysis, and genetic fingerprinting all point to low genetic differentiation between and within wolf populations (Brewster and Fritts, 1995). For example, in an analysis of 310 C. lupus individuals from 16 North American localities, Lehman et al. (1991; see also Wayne et al., 1992, 1995) found five C. lupus mtDNA genotypes widely distributed among populations, with only two populations (from Mexico and Manitoba) possessing one uniquely. Sequence divergence among genotypes was extremely low (<0.5%), with the most differentiation present in Mexican, Alaskan, and southeastern Canadian wolves (the peripheries of the North American range) (Wayne et al., 1995: 403). A similar pattern has been found for Old World C. lupus populations (Lehman et al., 1991; Wayne et al., 1992). Thus, consistent with the patterns of clinal variation and statistical overlap in morphological features discussed above, genetic analyses suggest “a large, panmictic (randomly interbreeding) population resulting from extensive movements of individuals and packs...” (Brewster and Fritts, 1995: 369), despite significant population differences in gross morphology detectable through multivariate analyses.

Although increasing geographic distribution is associated with greater species diversity in many genera (Foley, 1991), this is not the case among the wolf-like canids. Instead, across their extensive geographic range, these animals demonstrate minimal genetic differentiation, substantial clinal variation in body size and proportions, and affinities between widely separate populations—all against a backdrop of behavioral similarity and mutual mate recognition. Resistance to discontinuous regional differentiation appears to be a consequence of large home ranges, long dispersal distances, and a history of repeated waves of colonization across and between continents (Nowak, 2003). Recent molecular genetic analyses have been interpreted to suggest that gene flow has stifled genetic differ-entiation among C. lupus (Wayne et al., 1995; Wayne and Vila,
2003), as it has among *C. latrans* (Lehman and Wayne, 1991).

In the words of Wayne and Vila (2003: 236), “In this sense, typological species concepts may be inappropriate because geographic variation in the wolf is distributed along a continuum, rather than being partitioned into discrete geographic areas delineated by fixed boundaries.”

Could the same have been true of Pleistocene *Homo*?

**Species resilience in Canis and Homo**

Molecular clock estimates place the divergence of wolves, coyotes, and jackals at 2–3 mya (Wayne et al., 1995). Up to nine possible species of wolves have been identified in the fossil record since that branching point (Nowak, 2003: 240). Most of these represent chronospecies since the last common ancestor, with *C. etruscus* and then *C. mosbachensis* representing the best described earlier Pleistocene forms (Agustí and Antón, 2002). The relatively brief appearance of *C. dirus* (the dire wolf, about 30,000–10,000 ya) marks the only fairly clear period during which two contemporaneous wolf species were present in the fossil record, and some workers nevertheless consider *C. dirus* a large regional variant of *C. lupus* (reviewed in Nowak, 1979, 2003: 240). Fossils identified as modern *C. lupus* date to the late Middle Pleistocene in North America (Kurtén and Anderson, 1980: 171) and Eurasia (Nowak, 1992; Agustí and Antón, 2002). Hence, the previous emphasis on interspecific fertility in modern canids to illuminate possible hominid species relationships (e.g., Holliday, 2003) has neglected the equally interesting possibility that wolves are a model of resilience to allopatric speciation in a large terrestrial mammal.

Later hominids share with wolves the suite of behavioral characteristics that makes species resilience in the latter possible. The behavioral parallels between wolves and hominids thus represent strong theoretical support for the hypothesis that Pleistocene *Homo* evolved multiregionally as a single, widely dispersed, polytypic species (Wolpoff et al., 1984; Thorne and Wolpoff, 1992; Hawks et al., 2000; Cunroe and Thorne, 2003). The central proposition of this argument is that a large bodied, nutritionally demanding, adaptively flexible, eurytopic species would not have had the opportunity to speciate. This is because genetic differentiation would not have been necessary to colonize the new ecological spaces open to expanding *Homo* populations, and sustained vicariance would have been unlikely even if temporary periods of climate-driven isolation occurred during transcontinental colonization (Hewitt, 1999; Dennell, 2003). Other theoretical approaches have produced results consistent with this chronospecies interpretation (Foley, 1991: 421; Grubb, 1999: 163; Conroy, 2002).

Although it is clear that Pleistocene *Homo* comprised many distinctive morphotypes, both over time and contemporaneously, examination of the wolf-like canids suggests that caution is warranted in drawing species-level distinctions based on morphological variation. Likewise, the canid analogy suggests that caution is warranted in attributing the relatively low genetic variation documented among modern humans (Vigilant et al., 1991: Table 2; Goldberg and Ruvolo, 1997; Gagneux et al., 1999; Krings et al., 2000; Kaessmann et al., 2001; reviews in Relethford, 2001; Pearson, 2004) to recent common ancestry (Cann et al., 1987; Vigilant et al., 1991). In both wolves worldwide and coyotes in North America (Lehman et al., 1991: Table 4; Wayne et al., 1992), low genetic variation has been linked to persistently high levels of gene flow (Wayne et al., 1995). In view of the analogously eurytopic and mobile nature of Pleistocene *Homo*, the wolf-like canids provide a compelling demonstration of how gene flow could have stifled hominin, and eventually modern human, genetic diversity (Wolpoff et al., 1984; Relethford and Harpending, 1995; Hawks et al., 2000; Relethford, 2001; Templeton, 2002).

**Resilience to speciation versus competitive exclusion**

The use of a canid analogy to support a single species interpretation of Pleistocene *Homo* evolution differs fundamentally from the theoretical argument for Lower Pleistocene single species evolution proposed by Wolpoff (1971). The analogy to the wolf-like canids focuses on the conditions that favor, or do not favor, genetic divergence between parent and daughter populations. By contrast, citing the competitive exclusion principle, Wolpoff (1971) argued that there would not have been ecological space for two Lower Pleistocene hominid species to coexist because of the ecological overlap inferred from their reliance on tool use for hunting and defense. Both models envision broad habitat tolerance for hominids. But the key difference between the two approaches is that Wolpoff (1971) attempted to show why two culture-bearing hominid species could not have existed sympatrically, whereas the canid analogy asks whether under conditions of allopatry, which are assumed to have occurred periodically throughout human evolution as a consequence of normal and climate-driven dispersal and population movements (cf. Grubb, 1999), hominids would have speciated to begin with.

Significantly, persuasive theoretical objections to Wolpoff’s (1971) single-species hypothesis do not apply to the species-resilience hypothesis described here. Rather, they tend to support it. In his critique of Wolpoff’s (1971) argument, Winterhalder’s (1980, 1981) key insight was that hominin cultural abilities would have increased, not decreased, the potential for sympatry between competing hominin species, because the ability to make and use tools would have dramatically increased the potential of hominin populations to partition real ecological niches and, consequently, to coexist. By the same token, Winterhalder’s (1980, 1981) analysis of culture and niche partitioning supports the species-resilience interpretation based on the canid analogy, because if culture increased the potential for niche partitioning, it would by definition have increased hominin eurytopy. Following this reasoning, behavioral,

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6 Foley (1991) computed high estimates of hominid species richness based on comparative primate data, but low estimates based on comparative carnivore data.
not genetic, variation would have made colonization of new environments possible, further reducing the likelihood of vicariance and speciation.

**Problems and future directions**

The canid analogy presented here offers an ecological perspective on the question of species resilience in hominin evolution. Like all analogies, it is imperfect.

First, the utility of the analogy depends on the degree to which Pleistocene *Homo* were in fact mobile and habitat tolerant. For example, despite their adaptation for endurance locomotion, these hominids may not have habitually dispersed long distances as do the wolf-like canids. Resolving this issue will be essential for evaluating whether a *Homo* population could have become isolated in southern Africa (cf. Klein, 1999) or in Europe (Howell, 1952; Hublin, 1998) for the 0.5–1.0 million years necessary to speciate (cf. Avise et al., 1998), since dispersal corridors were present even during glacial maxima (Howell, 1952; Fig. 1; Turner, 1984: 195; Hewitt, 1999: 90; see also Simmons, 1999; Dennell, 2003: 427). Similarly, despite the increasing importance of meat to the hominid diet during the Pleistocene (Milton, 1999; Richards et al., 2000), the extent of dietary breadth among hominids remains unclear (but see Ungar et al., 2006).

A second challenge to the analogy is the degree of species resilience the wolf-like canids actually manifest. If *C. rufus* (or some other peripheral population) proves to be a good biological species, despite high levels of hybridization driven by extreme disparities in population size with neighboring wild *C. lupus* populations, then the canid analogy would support a multi-lineage scenario of Pleistocene *Homo* evolution (see: Mech, 1970; Lehman et al., 1991; and Wayne and Jenks, 1991, in support of *C. rufus* as a *C. latrans/C. lupus* hybrid; see Nowak, 1979, 1995, 2003 for *C. rufus* as a separate species from *C. lupus* and *C. latrans*; and see Wilson et al., 2000 for *C. rufus* referred to *C. lycaon* as descendants of an early colonizing wolf population separate from *C. lupus*). A similar conclusion might be warranted if *Lycaon* and *Cuon* spp. are referred to *Canis* (Werdelin and Lewis, 2005), or if jackal species are shown unequivocally to have split recently from the wolf-like canid clade (cf. Zrzavy and Lewis, 2005), or if jackal species are shown unequivocally separate from *C. lupus/C. latrans*. A similar conclusion might be warranted if *Lycaon* and *Cuon* spp. are referred to *Canis* (Werdelin and Lewis, 2005), or if jackal species are shown unequivocally to have split recently from the wolf-like canid clade (cf. Zrzavy and Ríčáňková, 2004). Finally, debate persists regarding the identification of fossil canids (Nowak, 2003), as it does for fossil hominids, and the current picture of *Canis* chronospecies could yet be reorganized into one that emphasizes a series of contemporaneous fossil lineages.

Finally, a “species resilience” perspective on Pleistocene *Homo* evolution offers the potential for new comparative analyses of modern species to explore constraints on the speciation process. It has long been recognized that eurytopic mammals tend to be more widely distributed and less speciose than stenotopic ones. However, detailed quantitative analyses of mobility, dietary breadth, and genetic variation within and between eurytopic species, in conjunction with fossil evidence, are needed to resolve more precisely the determinants of relative species resilience. Especially interesting would be comparative analyses of intercontinentally distributed carnivores such as ursids, felids, and canids, as well as of widely distributed primates. Coyne and Orr (2004: 425) note that relatively little research has been devoted to factors that prevent speciation. Comparative analyses of species resilience in *Homo* and other eurytopes, therefore, offer the possibility of contributing both to debates about hominid taxonomy and to our understanding of mammalian speciation in general (cf. Vrba, 1992).

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**References**


