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Reply to Professor Washburn

Sir:

(1) I do not understand why Washburn should overreact to my reference to a Lamarckian approach. My article was charitable in not pressing that issue further. I made it clear that I was not accusing either Washburn or Howell of Lamarckianism. My point was, and remains, that *as far as the analysis had been carried*, it was similar in a *structural* sense to a Lamarckian argument. I pointed out on page 64 that the authors had no such intention. However, simply listing items such as "language, memory, motor skills, foresight, complex social organization, and art" is only a form of hedging until these highly complex variables are brought into direct analysis and integration with what has essentially been left as simple replacement of function. The remaining quotes I gave, on pages 63–65, make it clear and certain that no attempt was made to make the simple substitution of function compatible with evolutionary and genetic theory. Effectively, then, no other real consideration of canine reduction *was* given, despite Washburn's reiteration of variables that he believes should cover the question.

(2) The most peculiar point of Washburn's paper is his rebuttal of dietary hypotheses. Washburn says that I suggest that the "sex difference in the size of ape's canine teeth may be due to diet. . . . " His letter then provides a number of observations to prove that diet had no part in this matter. It should be obvious that the abstract and first paragraph of my paper relate the differences to social behavioral variables. I repeat this theme again and again in text. On pages 64 and 65, I specifically note that Pilbeam and Simons suggest a dietary link, not I. On pages 64 and 65, I even mention Washburn and Avis (1958:425) *twice* in rebuttal of such a viewpoint.

Washburn carries the dietary theme even further when he imputes to me the suggestion that "since teeth are associated with diet, the large canines might adapt the males to some special kind of food." Would Washburn identify the correct party that made this suggestion? The quote is strongly reminiscent of the quotation I gave from Washburn and Avis (1958:425) in my article. A careful reading of that 1958 piece does not disclose where the dietary hypothesis came from.

(3) Washburn cathects on the word "hormone" and forgets to include the word "interactions," which I stressed in abstract, text, and footnote. The result is an unfortunate misrepresentation. I thought I had made it clear that I was not talking about hormones per se, but about the totality of interactions between hormones and target tissues. Obviously, the epigenesis of tissue is genetically different in the various primate groups, and it is hardly necessary to say that hormones alone will not convert apes into man. I certainly never made that inference. Washburn suggests that I regard early human evolution, and particularly sexual dimorphic decrease, as simply a matter of androgen reduction. I never said that. Nor did I say that "human sexual behavior differs from that of apes because of differences in hormones." What I said was that full-time receptivity of the female *plus* increase of relative (different rate and duration of growth) brain size *plus* a switch to a carnivorous diet (more so than before) *plus* a decrease in dimorphism (at least relative to the canines) implied endocrine changes in the past. Endocrine changes (interactions) were meant in a broad sense, and note 3, to which Washburn refers, made this clear. This could be a matter of timing, target tissue sensitivity, rate of growth, different feedback thresholds, etc. Genetic instructions for growth and development do not act in a vacuum. My purpose in raising the hormonal aspects was to suggest a link between behavior (in terms of aggression thresholds—which hardly excludes target tissues), social behavioral adaptations, and bodily concomitants of complex changes in hormonal–target tissue interactions during evolution.

My reference to aggression differences in different species and strains and to genetic selection for such traits cannot be construed as some simple idea that only androgens are responsible. Hormone interactions are extremely complex, and my lack of citations rests upon the joint facts that there is not much in the way of comparative primate endocrinology and that my article was reduced from 50 pages. In fact, the only reference I have found showing any direct relationship in teeth is Egami (1956). He showed that testosterone propionate inplants stimulated the growth of tooth length in female fish, *Orzyias latipes*, and that estrogens had no effect on male teeth. Garn *et al.* (1954) found sexual dimorphism to be the greatest in human canines, and suggested a Y-chromosome influence. Garn also suggested to me (personal communication) that the larger part of tooth size is autosomally controlled and that the magnitude of dimorphism forms a field, differentially effecting I2, P1, and C.[1] Garn *et al.* (1966) find strong correlations in brother-sister dimorphism in canine size, and even Washburn and Avis's (1958) listing of differences in primate canine length and body size indicates that there are obvious target-tissue specificities between body size and teeth in the same species. Garn's work suggests autosomal relations and perhaps even polygenic inheritance. Washburn might consider this possibility when he discusses both the reduction of canines to reduce the cost of intragroup fighting and his own field data regarding dominant male baboons that are most successful in inseminating the females during their most susceptible phase. His model is simply not compatible with genetic and evolutionary theory, unless he is willing to buy altruistic biogenic models of gene change and evolution, a position ably criticized by Williams (1966). Incidentally, there is an interesting study by Jacobs *et al.* (1965), which claims a relationship between XYY males and aggressiveness, also tallness. Welch *et al.* (1967) had difficulty in replicating these results, but found that the plasma testosterone levels of at least one XYY male showed a concentration four standard deviations above normal males. Welch pointed out that there might be a "dosage effect of genes governing the production of testosterone and located on the Y-chromosome" (p. 501). One must search wide and far for even this meager but suggestive data.

Washburn says: "The suggestion that hormonal changes caused the loss of canine adaptation affords no explanation as to how the functions of the canines were replaced." I don't believe I said that hormonal changes caused the loss of canine adaptation (whatever this may actually mean). I suggested that natural selection favored *behavioral* processes in such a way that one "strategy" (no plan invoked) resulted in canine reduction. As to how the canines were replaced, this requires a set of assumptions regarding their use in the past. My assumption placed greater weight on intragroup fighting and dominance than predator pressure. I mentioned this more than once in my article.

(4) In view of Washburn's newer statements on canines and selection, it is necessary to quote in full that part of Bramblett which refers to tooth attrition in baboons:

> In summary, all older male baboons exhibit much destruction around teeth by peridontal diseases.
> Often, but not always, this destruction is associated with damaged or carious teeth. All of the older animals have heavy tartar deposits. Caries occur, but attrition is the primary cause of tooth destruction and loss. The orderly pattern of attrition is used for estimating the ages of older members of the sample, and if these age estimates are accurate, tooth destruction limits the life span of the male to about 20 years. Female baboon dentition does not show as much extreme wear and loss [1967:332].

From this statement, Washburn concludes that the attrition between upper canine and lower premolar eventually acts to break the canine off, which is characterized as a frequent occurrence in baboons, seriously limiting the life of the male. A *non sequitor* then follows that selection should favor short canines. As interesting as Washburn's statements might be, they do not come from the Bramblett article above, unless there is other information that Washburn has gained ("personal communication.") Twenty years leave, I would think, considerable time for males to pass off *several times whatever genetic materials are associated with canine length,* and the suggestion that ones with shorter canines pass more genes than those with longer ones seems, in light of Washburn's own research, an odd kind of suggestion.

(5) Washburn claims that I dismiss the problem of why we became tool-users by calling it a "logical extension of a propensity." I hardly did this. My point was that primates are adapted for manual ability, as Washburn's flea-picking research has so deftly illustrated. Washburn is certainly correct, as Hall (1963) pointed out, that the instrumental use of objects is rare in mammals and primates other than man. Perhaps my wording was not precise enough. The fact remains, however, that the instrumental use of objects is far less rare in higher primates, which was my main point. In this regard, it is interesting to study the recent exchange between Washburn and Jay (1967) and Kortlandt (1967; see also Kortlandt and Kooij 1963) concerning the use of objects for agonistic displays, such as throwing and shaking limbs and branches, wielding clubs, etc. I fail to see why these should not be included as instrumental use.

(6) Similarly, the suggestion that I regard the instrumental use of objects as a simple process is somewhat annoying. I am very much concerned with its complexity. That is exactly why I stressed that substitutive replacement thinking (tools = canines) is far too simple, and that tool-making and -using in early human evolution was *one* outcome of a very complex and shallowly understood process of cognitive reorganization, involving brains, hands, and social and individual psychological factors. That is one reason why I mentioned Hallowell, Tappen, Hockett, and Ascher; for with these authors I share the view that symbolic behavior was involved in tool-making, and one can harldy avoid the brain and cognitive organization in this matter. Simplistic replacement of function of canines according to Washburn's orthodoxy entirely avoids this complex area.

(7) "The significance of the field studies cannot be dismissed by citation from secondary sources whose authors have neither taken part in behavioral investigations nor read the literature." This type of ex cathedra statement simply does not belong in science, and is unbecoming both to Washburn and to anthropology. Aside from the question of how Washburn knows who has or has not "read the literature," I remind him and the readers that with respect to predator pressure, I cite Washburn and DeVore (1961a and b), DeVore (1963, 1964, 1965), DeVore and Washburn (1963), Hall (1965), and Crook and Gartlan (1966). The main articles that Washburn includes all have a 1967 date, and I am not privy to any advance publications in the field of primate studies.

This statement of Washburn's raises some interesting questions. Is Washburn suggesting that only those who have studied primates in the field—or subscribe to his viewpoints—are entitled to ponder over the significance of the field studies for man's evolution and behavior or attempt to analyze the meaning of such data? If other scientists are not able to read such reports and apply them (if they desire) to their problem areas, ***such reports have no place in science.*** Washburn should avoid such sweeping statements and specify those sources he regards as secondary and those authors who are unfamiliar with the literature.

(8) Would Washburn clarify the significance of (a) knuckle-walking for sexual dimorphism and (b) the observation of leopards trying to get box-trapped baboons for predator pressure? Would Washburn back up his claim that man and baboon

are competitors in the savannah? Present-day field studies show that social behavioral adaptations are extremely varied and complex in both arboreal and terrestrial primates; each seems to be specific for the particular ecological surround in which it occurs. Baboons seem particularly variable in this regard (North, East, South Africa). Who is to say that the present situation is the same as that 1.5–2.0 million years ago?

(9) The question of "how long would a nonaggressive small-canine species survive unprotected in the African savanna" suggests that Washburn missed my point. Did I say they were unprotected? My point was that *intragroup* aggression probably diminished and that more cooperative aspects of group behavior were favored, along with intelligence. This does not mean that early hominids were unaggressive, particularly in terms of extragroup behavior, or that particular clusters of sign stimuli generated within the group would not be met by aggressive responses. Washburn comes to that conclusion because of his prior misunderstanding of what I meant by hormonal interactions, a logical outcome if one is thinking only in terms of decreased androgens. Did I mention Etkin's two papers for nothing, that is, that the main problem was cooperative intelligent behavior? I made it clear that I thought natural selection favored a different constellation of individual and group social behavior during hominid evolution, and that both tool-making and reduction in canine dimorphism (plus possible increases in other interesting anatomical features) were but two results of such selection. I am more inclined to consider that the functions of the canines were "replaced" by changes in social behavior, not tools.

(10) Washburn says: "Once the weapons had evolved to a point at which they were more effective than teeth in intergroup conflict, in species spacing, in protection from predators, and possibly in hunting, then selection might be for small canines, which would reduce the cost of ingroup fighting." Was this point pebble tools or stick-throwing? Again, why not keep the canines? It now turns out that they are disadvantageous to the group because baboon studies show that these inflict terrible slashing wounds. (Yet see Bramblett's article regarding healing.) I prefer N. A. Drekopf's (personal communication) theory that the canines were reduced to facilitate mouth-to-mouth kissing, or to prevent the tongue from getting bitten in two during primeval symbolic mouthing (the origin of language). Frankly, Washburn's newer position seems to go against his own researches on dominance and insemination and also against the fossil evidence. The admittedly fragmentary evidence of *Ramapithecus* implies that the canines were reduced *prior* to the time when stone tools came into existence—at least in their manufactured form. According to Washburn, however, *Ramapithecus* might be a pigmy chimpanzee, so that takes care of the matter. The dental remains of *Australopithecus* (including the so-called "habilis") show that the canines are human in shape and size. Where, then, did this intragroup selection take place that Washburn is talking about? The two questions regarding implicit assumptions in the orthodox position on canine reduction remain unanswered. "For this widespread and long-lasting adaptation to be reduced, the functions that the adaptations has performed must change or be performed in some other way." If the canines were there, why did the tools *have* to supplement and eventually replace them? The tools were apparently serving the canines' function, but we are left without any explanation as to why or how the tools are used so effectively that the canines start reducing. Washburn does not suggest any anterior selection for structures or behavioral organization that allows for this grand replacement of function of the canine adaptation.

(11) The above quote appears to be based on Washburn's view that Goldschmidt's "comparative functionalism" is a new godsend to the problems of primatology. Not being a cultural anthropologist, I cannot speak about the value of this work for cultural anthropology; I note, however, that a number of cultural anthropologists seem to feel that there is nothing new in the theory beyond Durkheim or Malinowski, and that one is without any definition of what "function" is (see Murphy 1966, for example). Washburn claims that the theory will "help avoid the use of very general terms with no clear referents to serve as guides to further observations and experiment." Perhaps the theory's real usefulness *is* for primatology, but this is hardly demonstrated in Washburn's letter. Actually, what the quote given above accomplishes is quite simple: it simply rules out the possibility that selection may have operated on behavior, or on some set of variables we have thus far neglected; it denies the possibility of positive selection for anything else *but simple replacement of function.* In short, Washburn's assumptions and statement of the questions and problems leave no other alternative—he has built the answers into his questions. This may be new in primatology, but hardly seems new in functionalism. By his own logic, where he is championing the importance of the canine for intragroup conflict, and tools for predators, selection should also have favored tools that did not cause lethal injuries within the group. This logical extension is directly relatable to the nature of Washburn's assumptions regarding functionalism and his disregard for the complexities of behavior that underwent selection.

(12) One of the most interesting aspects of behavior in terms of prey and predator is the relationship between certain motor patterns, defensive or aggressive displays, etc., that effect the predator's advance or effectiveness. Estes' (1967) piece on the predation habits of carnivores, particularly felids in Africa, is interesting in this regard. It turns out that the prey have a considerable inhibiting effect

on the predator if they (in mixed or separate groups) directly face the predator. It does raise some interesting questions of possible critical sign stimuli that are part of an animal's behavioral repertoire serving to inhibit attack. Recent evidence for predator pressure should be weighed against these and other variables. Washburn reiterates in his letter the spirit of a comment made by DeVore and Hall:

> During a year's field study it is unlikely that actual predation on baboons will be seen. . . . Finally, it should be remembered that the removal by predators of only a few individuals annually from a sizeable population would be almost impossible to detect during an average study, yet would exert very important selection on the evolution of the species [1965:49].

For anyone who has thought much about population genetics, it is obvious that such arguments should rely on the application of population genetic models to assess the theoretical possible shifts in gene patterns through such a selective agency. Given that this assertion might be the actual case, the situation is equally logical if one substitutes "intragroup fighting," "accidents," or "disease" for "predators." The acid test for evaluating the importance of these various factors is observation. I gather from Shultz's publications and Bramblett's work that disease, parasites, and accidents cannot be dismissed, and, from what I have read, intragroup and intergroup fighting is hardly of little importance. I find the literature on primate disease incidence to be of great interest, particularly in the light of current research tending to relate disease resistance, the endocrine system, mortality and fecundity, aggressiveness, spacing, and density (see Christian *et al.* 1965, for example). If I may be permitted some further speculation, I again suggest that there is profit in viewing early hominid evolution as a "revolution" in social behavior, based largely on reorganizations of physiological functioning—including the endocrine and nervous systems—such that a number of morphological and behavioral changes could be viewed as a parcel of integrated "strategies" in line with ecological variables and successful adaptation. I suggest that an endocrine shift occurred in the direction of greater group cohesiveness and cooperation, which had *manifold* effects: an extension of growth (a reduction of the inhibitive androgen effects on growth), extended postnatal care, domestication of the male, full-time receptivity of the female. To this I add the following suggestions: (a) a reduction in aggressiveness to allow closer spacing and increased social interaction, and (b) incorporation of protein-intake through hunting to maximize energy relationships, growth, and possibly disease resistance. One possible outcome of such a process would be a reduction in canine dimorphism, as well as *increases* in other dimorphic features (such as the breast, buttocks, fat distribution, and perhaps behavior).

(13) Finally, I would like to take up Washburn's comment to the effect that we do not disagree very radically. The sort of altruistic biogenic selection models he offers in his letter to explain why the canines should reduce is one reason for our disagreement. More to the point, I do not believe that we are getting very far by making such obvious statements as: "the differences between man and ape are the result of changed selection resulting from a progressively different way of life. . .," or "social structure may also be in part an adaptation to predation." I feel it is our problem to synthesize the generalities with anatomical, physiological, and behavioral specifics at some more detailed levels that do not violate our modern understanding of genetic and evolutionary frameworks. Washburn's letter suggests that we are not simply quibbling over a small detail—how a tooth got smaller—but are arguing over basic assumptions and perspective. I am less concerned that my position regarding hormone interactions be accepted or rejected than that the complexity of early human evolution be appreciated. My major point was that the orthodox explanation given by Washburn to explain canine reduction is too simple and neglects large areas of complexity. Washburn's letter does not change my mind on this.

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NOTES

[1] Garn also questions (personal communication) whether there was any very great reduction in canine size during early human evolution. In other words, that we come from a long ancestry of small-canined animals. In my discussion of reduction, I have been assuming that the reduction might have been on the order of the difference between man and chimpanzee, whereas Washburn seems to feel that the difference was far greater—on the order of baboons and man. Perhaps this is an unfair assumption on my part, but I tentatively hold it in view of his stress upon baboon studies and predator pressure. Garn's point is very important and deserves far greater thought than heretofor given.

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