

Human Ethology Newsletter

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SOCIETY NEWS

Toronto Congress

The twelfth ISHE congress will take place in Toronto 3-7 August. It is too late to submit an abstract to present a paper, but abstracts for posters are still being accepted. Send your poster abstract (250-word maximum) to both Linda Mealey (Psychology Dept., College of St. Benedict, Collegeville, MN 56321 USA, tel. 1-612-363-3135, and Irwin Silverman. Contact Irwin for information fax. 1-612-363-3202, E-mail LMEALEY@csbsju.edu) on attending the congress: tel. 1-416-736-5122, fax 1-416-736-5814, E-mail ISILV@VM1.YORKU.CA.

The congress program, being arranged by Linda, promises to be an exciting one (see accompanying tentative schedule). More than 40 papers have been accepted. About 60 people will be in attendance.

The methods workshop is conceived by Nancy Segal as follows:

Ethological interpretations of human behavior lend a fresh perspective to standard laboratory methods, interviews, and questionnaires. The interdisciplinary nature of human ethology naturally invites the generation of novel research designs to address questions that arise within each investigator's special area of interest. Researchers conducting ethological studies (observational or not), or who anticipate supplementing ongoing projects with ethological analyses, are encouraged to discuss their work in an informal setting. The

emphasis will be on new research designs (or improvements in standard methods) that have been applied or are in development. Slides, videotapes or other audiovisual materials will be welcome.

Nancy will start the workshop by discussing her own study of genotypic and gender influences on cooperation, using twin children with unfamiliar partners, as well as a study in progress which examines the common genetic contribution to spatial proximity and social relatedness in a free play setting.

Bill Charlesworth's teaching workshop is taking shape along these lines:

It is important for instructors in an emerging cross-disciplinary field, such as human ethology, to increase formal recognition in teaching institutions in two ways: (1) by inserting a course in human ethology into established curricula, and (2) by including it as a section in appropriate existing courses. In both cases, explicitly articulated teaching strategies and tactics are crucial. Content, textbooks, a rationale for including human ethology with existing programs, substantive connections with adjacent disciplines, teaching and assessment methods, etc. have to be spelled out clearly. Workshop participants will share ideas on how this is currently being done, and discuss ideas for "universal" criteria on how it should be done.

Bill will start the workshop by discussing his own thoughts based on 20 years of teaching. Roger Masters will follow with a presentation on the new Gruter Institute Reader--an evolving collection of readings that can be tailored for classes relating to human ethology, biology, law and politics. Please

bring your own syllabi, reading lists, questions, and ideas for teaching human ethology.

There will be two **business meetings**. The first is open to the general membership. It is intended as a forum for members to raise issues to be discussed by the officers at the second business meeting.

To prepare for this first meeting, please try to brainstorm (or "brainwave") about how to improve the Society. What sort of conventions should we have? What other societies, if any, should we try to work more closely with? Do we need to change the officers' duties, or elect additional officers? How can the newsletter be improved? Should a new editor be appointed for the next two-year term? How can international communication be expedited? Should the Society become more active in promoting evolutionary views of human behavior? If so, how?

Members are encouraged to express their views to the officers informally throughout the congress also. The first business meeting is designed only as a stimulus to continued, informal discussion.

Membership Renewals for 1994

It is time to renew your membership for 1994 if you have not already done so. Membership is by calendar year, so dues are to be paid by the first of the year. **If the date on your mailing label is earlier than the current year, it is time to renew your membership.** For economic reasons, renewal notices are not sent. Those who do not renew their memberships will be removed from the membership list. Please report any errors, change of address, etc. to the editor. Current dues and directions for payment are given on the last page.

CONGRESS SCHEDULE

Wed., 3 Aug.	Thurs., 4 Aug.	Fri., 5 Aug.	Sat., 6 Aug.	Sun., 7 Aug.
		MORNING		
(Registration begins 2 Aug.)	M. McGuire, "Envir. contingencies and physiol. change"	K. Grammer, "Body talk between strangers of opposite sex"	Gary Johnson et al. on politics	Brain and behavior
Environment & behavior I	Psychiatry I	Gender signals	D. Freedman on attachment	Officers' meeting
		AFTERNOON		
Environment & behavior II	Psychiatry II	Gender dynamics	Development	
General business meeting	N. Segal, methods workshop	W. Charlesworth, teaching workshop	W. Charlesworth, "Human ethology a good idea for the behavioral sciences and society"	
		EVENING		
Reception, posters	Banquet	Barbecue	Social event (Niagara Falls?)	
I. Eibl-Eibesfeldt, "Contributions of human ethology"				

Nomination of Officers

The terms of the Secretary and the Membership Chair are up at the end of this year. The Secretary is Karl Grammer and the Membership Chair is Nancy Segal.

Because Nancy will be running for another term, she will not properly be able to coordinate the nomination process. Instead, Barbara Fuller, our Treasurer, has agreed to handle this assignment.

Please submit nominations to Barbara at the School of Nursing, University of Colorado, 4200 E. Ninth Ave., Denver, CO 80220 USA; tel. 1-303-270-8929; fax 1-303-270-8660. Please include the nominee's name, address, and telephone number, if possible. Self-nominations are encouraged. Barbara will contact nominees to ascertain their availability. There are no official requirements for geographic or disciplinary diversity for the officers, but obviously such diversity is desirable. Nominations close 15 August.

Dues Payment Screw-ups

There have been more foul-ups than usual in the recording of dues payments for the Society. We believe that one list of payments was lost in the mail between Treasurer Barbara Fuller and Membership Chair Nancy Segal, resulting in about 15 such failures. Members have been unfailingly patient and courteous in notifying us of these slip-ups.

Inevitably, our updating of members' dues status lags behind payments. Please continue to bear with us as we take, sometimes, several weeks to catch up. If, however, two issues appear without your dues payment having been registered, please send the treasurer a gentle correction.

Membership Directory

All those who have renewed their membership in ISHE for 1994 will be listed in the Membership Directory soon to be prepared. Nancy Segal, the Membership Chair, has agreed to compile the directory. If you have not yet paid your dues (last calendar year through which you are paid is given on your address label), please complete the form on the last page. If your dues are paid up, please complete the form on the penultimate page (or a photocopy thereof).

Yes, I know that the pages are back to back. I assume that you will want to save and treasure your newsletter issues, and will make photocopies rather than mutilate the original. However, it is all right to send the single page, with both sides filled out, to Barbara. That way I won't find out who you are.

Members may now pay by credit card (VISA, Master-, or Eurocard). Please use this method if at all possible, as it saves us currency conversion charges.

Newsletter Submissions

Anything that might be of interest to ISHE members is welcome: Society Matters; articles; replies to articles; suggestions; announcements of meetings, journals or professional societies; etc. These sorts of submission should be sent to the editor. Book review inquiries should go to the appropriate book review editor (the British editor covers English-language books published in Europe). Submission should be in English, on paper and, if possible, on diskette. Please include complete references for all publications cited. For book reviews, please include publisher's mailing address and the price of hardback and paperback editions.

No material in the newsletter is selected by critical peer review and thus material is presented only to foster free and creative exchange of (even outrageous) ideas between scholars. The fact that material appears in the newsletter never implies the truth of those ideas, ISHE's endorsement of them, or support for any policy implications that might be inferred from them.

Library Subscriptions

The number of libraries that subscribe to the newsletter is down. Accordingly, we have abolished the higher, institutional rate for membership in ISHE. Hereafter, libraries may join for the usual rate of \$20 per year, \$50 for three years.

It would help ISHE enormously if each member would complete the form on this page asking his or her university library to subscribe to the newsletter.

ARTICLES

A Markov Distinction: A Defense of Darwin's Honor

By Wade C. Mackey and Gilbert Garza, 9713
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In their article, "Differential fertility and the distribution of traits: The case of I.Q.," Preston & Campbell (1993) have offered the following argument:

Let us assume that a continuous, non-

discrete trait is influenced strongly by genetic material (Preston & Campbell use I.Q. as their trait). Both central tendency (mean) of the group and differences (variance/heritability) between individuals reflect genetic inheritance.

Let us also assume that total (100%) phenotypic endogamy occurs within specified subgroups. Individuals marry only within their own phenotypic (I.Q.) subgroups.

Let us further assume that there are constant and large differences in fertility among the subgroups. The subgroup with the smallest phenotype (lowest I.Q.) always has more fertile, viable offspring than does the largest phenotype (highest I.Q.). The average phenotype (average I.Q.) has an intermediate number of children, always.

Therefore, over time, the mean phenotype of the group may *rise*, or *fall*, or *remain the same*. Preston & Campbell invoke the considerable powers of matrix algebra to prove their point, and then rest their case.

Well, at first, second, and third blush, Preston & Campbell seem to have dismissed Darwinian evolution. Given a quantitative phenotype with strong genetic penetrance, perfect knowledge of differential fertility, and as much time as one might want to specify, the result would be zero predictability of the

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Please enter a library subscription for the *Human Ethology Newsletter*. Published since 1974, the newsletter contains articles, discussion, book reviews, announcements, and lists of current literature in the field of human ethology and sociobiology. The newsletter appears quarterly and is about 20 pages in length. The *Human Ethology Newsletter* is published by the International Society for Human Ethology, a not-for-profit scholarly society. A subscription includes a copy of the membership directory. A free sample copy is available from the editor, Dr. Glenn Weiseld, Dept. of Psychology, Wayne State University, Detroit, MI 48202 USA. The price for libraries has been reduced to \$20 per year (\$50 for three years) and includes air mail postage.

To subscribe for the current calendar year, please send library name and address and payment to Prof. Barbara F. Fuller, ISHE Treasurer, University of Colorado, School of Nursing, 4200 E. Ninth Ave., Denver, CO 80220 USA. Please pay by check in US funds made out to "ISHE" or by credit card (VISA or Master/Eurocard).

(Signature and Affiliation)

distribution of that trait within the group.

Wow!!! Were a discussion of this article and its implications to crop up at Wal-Mart, the faculty lounge, or a Departmental meeting, an ethologist whose knowledge of matrix algebra had understandably lapsed might be placed in an embarrassing position. Therefore, a rejoinder is hereby offered to mute those adhering to the Preston & Campbell position.

In their model, Preston & Campbell assume (a) a "primitive" matrix of reproductive histories and (b) a Markov distribution of I. Q. phenotypes. With these assumptions, their model will do exactly as they posit. Hence, Darwinian evolution looks superfluous--a conclusion that perhaps most sociologists would find comforting as well as useful (see van den Berghe [1991] for a most penetrating discussion).

But let us examine some of these assumptions. Preston & Campbell construct their (Markovian) model with zero *mortality* (the flip side of fertility) prior to reproductive age--an unrealistic assumption. In addition, there is perfect *monogamy*--everybody gets married. Lastly, there is perfect phenotypic endogamy for the subgroups. Mating systems are rarely that impermeable. A violation of any of these three dubious assumptions dissolves the Markovian magic and renders the Preston & Campbell model null and void.

We hope that this rejoinder proves useful at Wal-Mart, in faculty lounges, and in any other settings where Darwinism is discussed.

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Symmetry and Beauty

By David G. Hays, 25 Nagle Ave., Apt. 3-G,
New York, NY 10040 USA

I have recently (1992) suggested that the four quadrants of tertiary cerebral cortex, at least in bearers of modern cultures, are specialized to pursue the cybernetic goals of beauty, truth, love, and justice. If there is anything to this idea, the specializations must be due in part to the specific access that each area has to secondary and primary cortex and to

subcortical nuclei, and in part to learned cognitive skills.

Current work by Randy Thornhill and colleagues at the University of New Mexico, and by several other investigators, was reported in the *New York Times* Science Section on 9 February 1994. Briefly put, animals with symmetric bodies, and in humans symmetric faces, are preferred for sexual intercourse. The investigators suspect that genetic fitness is demonstrated by a well-formed body.



These two photos illustrate the powerful effects of genes on behavior. In the photo above, **twin brothers** Richard (left) and Leonard Oleszek, 55, of Milwaukee, Wisconsin, USA are shown. They both broke their **left ankles on the same day**. Richard sustained his injury when he fell off a ladder; Leonard broke his ankle when he slipped and fell on ice.



This photo shows Rosalyn and Marvin Schindler of Detroit, Michigan, USA. They are married to each other and both teach at Wayne State University (doubtless an illustration of homogamy)--but of course are **not blood relatives**. Accordingly, they broke **different ankles on different days**.

The work on symmetry provides an explanation for the goal of beauty. For the other quadrants, explanations are ready to hand. Truth is needed in cognitive, and especially in communicative, systems. Love is necessary for the care of infants, and for long-term adult bonding. Justice is necessary in social groups, lest some members contribute without recompense; whatever injustices we see, without some degree of equitable compensation social groups break up.

Aestheticians have suggested many times that some kind of coherence is the underlying requirement for the experience of beauty; in some sense never made very clear, the parts of an object must be suited to each other and to the whole. Symmetry is as elementary a concept of coherence as I can imagine. As for aesthetic experience, it seems to me that a more elaborate explanation is required; an epiphany must be the culmination of a sequence of several steps involving, typically, the experience of beauty in some but not necessarily all of them.

The explanation of my untested hypothesis about beauty by recourse to a hypothesis about symmetry that its proponents put forward only with reservations on account of the small amount of evidence collected thus far is, of course, a dubious step. I offer these comments in hope that they will stimulate some ethologist to test some part of the whole.

Reference

Hays, D. G. (1992). The evolution of expressive culture. *Journal of Social and Evolutionary Systems*, 15: 187-215.

Pheromones and Gay Liberation

By Roger D. Masters, Department of Government, Dartmouth College, Silsby Hall, Hanover, NH 03755 USA.

New research suggests the startling possibility that oral contraceptives may be related to the gay liberation movement. How

could women taking the pill lead homosexuals to come out of the closet (and perhaps even increase the frequency of homosexuality)? The connection is not as absurd as it may seem, though it depends on a hidden effect of contraceptive technology.

As Ackerman notes (1990), humans can smell as little as 3.2×10^{-15} of an ounce of animal musk, a pheromone close to human testosterone. Since the sensory cells in the olfactory bulb are directly connected to the limbic system (the pathway may have as few as two neurons, short-circuiting the neocortex), we can be influenced by such odors even if we are not conscious of them.

Males produce two related substances that have opposite effects on females. One, smelling like sandalwood and called androstenol, is perceived as pleasant, whereas the other, androstenone, which has an odor like urine, is repulsive to women. While both are associated with sweat, their exact relationship is not entirely clear. But since the negative pheromone, androstenone, seems to be more prominent, a recent study of its effects (Grammer, 1993) deserves attention.

We think of sexual interest as being "turned on," but androstenone has the opposite function. Because the human female, unlike chimpanzees or other primates, is always sexually receptive, a pheromone that inhibits female sexual attraction should not be surprising. Given the costs of pregnancy to human females and the absence of a period of heat, such a pheromone is particularly important in explaining the formation of lasting pair bonds.

As Fisher has argued (1993), males and females also have complex nonverbal cues that signal sexual availability and interest, leading to an overall pattern of serial monogamy. If pheromones were selected as a proximate mechanism favoring this mating system, we might predict that, at the time of ovulation, the inhibitory effects of the negative male pheromone would be reduced.

Grammer (1993) finds that this is exactly what happens. A sample of women exposed to androstenone under experimental

conditions generally rated the odor as unpleasant. But women who were ovulating at the time of the experiment gave the pheromone a neutral rating. Instead of being turned off by the negative pheromone, at this time of the month women were more "available" chemically for positive stimulation.

To understand the effects of such pheromones, however, it is necessary to consider them in the broader context of the socio-economic and cultural variables that shape the costs and benefits of sexuality (Tiger, 1987; Posner, 1992). Oral contraceptives have reduced the risks of heterosexual behavior. Today, premarital sex is normal; a generation ago, it was inhibited by the male's fear of a shotgun marriage and the female's fear of unwanted pregnancy or abortion. With the availability of the pill, women can for the first time control their fertility. This makes it possible for women to participate equally with men in the job market (at least until childbirth). Economic competition between the sexes obviously led to demands for equality of gender. Middle class couples marry later, many women postpone child-rearing, and before marriage couples often live together--and sleep with each other--for years.

In this context, the unconscious effect of the pill on females' reactions to male pheromones might contribute to a number of apparently unrelated aspects of the sexual revolution. Chemically speaking, oral contraceptives mimic the effects of pregnancy. Unlike women who aren't using the pill, Grammer found that during the proliferative period of the menstrual cycle, women taking oral contraceptives did not show the effects of androstenone just described. Women taking birth control pills had typical negative reactions to the male pheromone during menses and the secretory phase of the menstrual cycle, but instead of feeling neutral toward the male odor during ovulation, they rated it as slightly more negative. Perhaps not surprisingly for a drug that imitates pregnancy, the pill has the effect of making it harder to arouse a woman sexually for an important part of each month.

This effect need not influence positive odors to which a woman is accustomed, not to mention her attitudes toward specific men. But at the unconscious or instinctive chemical level, women taking the pill may strike males as

more turned off during a phase of the monthly cycle when they would otherwise be most receptive. This effect would be especially important in responses to unfamiliar men.

If oral contraceptives also influence the production of female pheromones--odors which attract males by signalling sexual interest--this effect would only strengthen the role of chemistry in the sexual revolution. Although these female odors do not seem to have been studied, effects depending on male sensitivity to pheromones are probably weaker than those depending on women's reactions. While there is considerable variation in the sense of smell from one person to another, as Ackerman notes, there is an overall tendency for women to be more sensitive to odor than men. Males tend to use visual cues when "looking over" potential partners; women seem to be more influenced by odors. It follows that pheromones are more likely to influence women than men. Given the dominance of males in our scientific community, this might explain why the phenomenon has received so little attention.

The unconscious chemical signals influencing sexual behavior obviously have an effect on social customs. When a man showers and uses a deodorant or after-shave lotion before going out on Saturday night, he obviously masks the androstenone which might otherwise turn off the women he meets. Could the use of oral contraceptives have changed the way such pheromones influence the sex lives of Americans?

Among primates, it is ultimately females who choose males. For humans as well, males seeking a sexual partner typically compete with each other for status or dominance; females then are attracted to the more successful males. If the effect of the pill is to increase negative reactions to men at a time of the monthly cycle when women would otherwise be "available," the system is changed. For males, at the chemical level, it is as if the sex ratio had been changed so that there are fewer women in society. In short, imagine the pill as having created a society with only eight or nine women for every ten men.

In an environment like this, the most competitive and aggressive males are likely to be successful in attracting women. Those who

are less aggressive or less self-confident, however, may feel unconsciously that they are rejected by women in general. Like boys in the traditional all-male private schools or those in such typically all-male social institutions as armies, prisons, and monasteries, the choice is often sexual abstinence, prostitution, or homosexuality. Gay behavior is more likely--or at least more likely to be treated as acceptable--in situations where heterosexual options don't exist (Posner, 1992).

For women who say openly that they prefer other women as partners, moreover, the emergence of lesbian life-styles as an alternative to marriage seems to follow the presumed effects of the pill. At the ideological level, radical feminism seems an exaggerated version of the chemical effects Grammer describes. If women using oral contraceptives are more likely to have an instinctively negative reaction to males, is it surprising that, on the conscious level, some feminists give voice to a correspondingly harsh view?

Although not everyone is influenced by a drug in the same way and not all women use oral contraceptives, in an environment of apparent sexual promiscuity even a relatively small effect could have a big influence on the approximately 3-4% of young men who report homosexual preference (Fay et al., 1989). Paradoxically enough, moreover, the sharp conflicts over homosexuality could well have been increased by the way the pill has led to almost universal sexual activity during the high school years. In a recent poll at Martha's Vineyard High School in Massachusetts, for example, over 80% of boys and over 70% of girls were sexual active by their senior year. Precisely because most males are able to "score" (to use the current slang), the few who fear they will not be successful in attracting girls seem somehow "queer" to some males who are more competitive or less fearful of sexual failure.

Although some studies seem to show an increase in the number of gays over the last generation, these results are often contested (Fay et al., 1989). As homosexuals come out of the closet, perhaps there is simply more honesty and better reporting of a constant level of homosexuality. On the other hand, it is also

possible that the reversal of traditional prejudices against "queers" and "faggots" has led to an increase in homosexuality, as many conservatives fear.

The argument that pheromones have played an important role in the sexual revolution is consistent with either possibility. The main point is that today some males openly behave as if there were fewer females around, while some females behave as if there weren't enough sexually available males. Such a paradox may be due to cultural attitudes that are just a historical accident, but human ethology suggests good--albeit sometimes paradoxical--reasons for the way humans behave. Just as the refrigerator can be described as a "divorce-making machine" (Masters, 1993), it is possible that the pill has been a major factor in the gay liberation movement.

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The Reversed World of the Spotted Hyena

By Frans Roes, 127 tweehoog, 1016 RK Amsterdam, The Netherlands

Except for humans and some of the eusocial species (such as termites and naked mole-rats), there are remarkably few species that form large, territorial, multi-male, multi-female groups. Most species living in such groups have a hierarchical social structure, with a few males dominating other group members. Social life is heavily influenced by what is best for the reproductive success of these males. Polygynous, harem-like structures are often the result.

Spotted hyenas (*Crocuta crocuta*) live in large, territorial, multi-male multi-female groups ('clans'), with a primate-like social system. The species is matrilocal; females remain in their natal group for life, unless a fission occurs (Holekamp et al. 1993). Young females with dominant mothers soon dominate females from lower-ranking matriline. Males leave their natal group around puberty, to join a population of nomadic males, before settling in a new clan. The spotted hyena is perhaps the only species living in the above-mentioned sort of groups, where females are clearly the dominant sex (for an explanation of this female dominance, see Hofer & East 1993a or 1993d). A single female hyena is able to prevent up to eight males from feeding on a carcass. As could be expected, social life is heavily influenced by what is best for the reproductive success of females.

One aspect of spotted hyenas that has fired the imagination of naturalists way back to the days of Aristotle is the 'pseudo-penis' of females. It is a very enlarged clitoris, with a false scrotum that contains fatty tissue forming two swellings easily mistaken for testicles. The 'pseudo-penis' can also be erected. The whole thing is an almost perfect imitation of the male genitalia. Its existence is explained as partly the result of high androgen levels in females, but Hamilton et al. (1986) and others insist that such a large and vulnerable organ cannot have evolved solely as an accidental side-effect of hormones, and even Gould (1981) seems to agree on this point.

Kruuk's explanation (1972: 229) of the 'pseudo-penis' is in my view both logical and spectacular. While referring to Wickler, he draws attention to 'appeasement' behavior of baboons. The 'presenting posture' is used by female baboons not only in copulatory behavior, but also as a general act of appeasement toward dominant males. To appease, females present their genitalia. As such, the posture is also used by males and juveniles. Kruuk mentions that male Hamadryas baboons are adorned with the typical red swelling that in other species is only possessed by (estrous) females. Apparently, reproductive success of male Hamadryas baboons is enhanced if they can appease other--typically dominant--males, by mimicking the female genitalia. Kruuk's suggestion is that this mimicry is a parallel to what evolved in the female spotted hyena. That is, in the multi-male, multi-female hierarchical Hamadryas groups, where the male sex is dominant, submissive males 'appease' dominant males by presenting a mimic of female genitalia. But in the spotted hyena, where females are dominant, submissive females appease dominant females by presenting a mimic of the male genitalia.

This idea seems fully supported by the fact that when two hyenas meet, it is the submissive animal that first presents its erected penis (real or pseudo), and even cubs have an organ almost as large as those of adults, which erects while greeting adults.

The hyena world seems turned upside down in several other respects. Consider a species where females do most of the parental investment. If males invest little in offspring, a male typically has a higher potential reproductive success than a female has. One male may sire many young, but when females must invest a lot in each individual offspring, the maximum number of offspring a female can produce is limited. In species where the female's parental investment exceeds the male's, it is therefore often found that:

- (a) Males are heavier, larger, and more aggressive, and have special ornamentation such as conspicuous feathers or weapons such as antlers. These features have evolved as a result of male-male competition for the scarce reproductive capacity of

females.

(b) Males are weaned at a later stage than females, so they are better prepared for male-male competition.

(c) For the same reason, males sexually mature at a later stage than females.

(d) Males die earlier than females, as a result of male-male competition (Alexander 1979: 33: 'The expected strategy is to start more males and save only those most likely to be successful'), and as a result of earlier senescence, associated with high reproductive capacity earlier in life.

Female spotted hyenas do virtually all of the parental investment, yet the literature suggests that for this species these patterns are reversed:

(a) Though linear dimensions do not differ significantly, females are heavier (55 vs. 45 kg) and more aggressive than males.

(b) Female spotted hyenas are weaned after 14-18 months, males after 12-16 months (Hofer & East, 1993a: 9).

(c) 'Both sexes reach sexual maturity just after they are fully grown, the female somewhat later than the male (Matthews 1939)' (in Kruuk, 1972: 29).

(d) 'Female hyenas disappear at a slightly faster rate than male hyenas' (Kruuk, 1972: 31). Hofer & East (1993b: 551) report 1.17 females per male, but this is not necessarily inconsistent with females dying earlier than males.

Furthermore, when females do most of the parental investment, one would expect at least some outright aggression between males. This has never been witnessed. Yet males are reported to be highly polygynous, one male siring a disproportionate number of cubs. Frank (1986: 1524) goes so far as to state that the size monomorphism of spotted hyenas is incompatible with sexual selection theory. Such a remark should guarantee the continual attention of evolutionary theoreticians to the spotted hyena.

Are male spotted hyenas in some way or another 'exploited' by females? As the sole function of males in the reproductive process seems to be to inseminate females (and they

don't even consider competing among themselves for that), one would expect in females, being the dominant sex, the evolution of traits that enable them to use the behaviour of subordinate males to their own advantage.

Alexander and Noonan (1979) argued that concealment of ovulation in humans correlates with a massive increase in male parental care. Male spotted hyenas clearly exhibit no parental care but, rare among animals living in multi-male multi-female groups, is the fact that females have 'concealed ovulation'. Overt morphological or behavioural changes that a female is approaching estrus have not been detected (Frank 1986: 1520). Apparently, this forces males to monitor females assiduously to avoid missing the brief period of receptivity. Males may persistently follow a female for as long as 40 days. One would expect dominant females to be more attractive to males than low-ranking females, as dominant females have shorter birth intervals, and as the offspring is very likely to be dominant again. If this is true, what use could it be to a dominant female to be trailed by a group of males?

A wild guess would be that a female, through their concealed ovulation, induces males to accompany her while she goes hunting. Once the prey is caught, it is of course the female who feeds first and most. (Because of her intense parental care, food is much more important for females than for males. The protein content of hyena-milk is the highest recorded, Hofer & East 1993d: 584). Kruuk (1975: 77) wrote: "Hunting packs consist of only one or two females and many males -the matriarchs take initiative, others follow". Could this be the dominant female with her daughter, followed by a group of male 'helpers'?

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REPLY TO AN ARTICLE

Frans Roes' "Parents' Preference for Their Offspring's Sex"

By Guy Richards, 327 666 Leg in Boot Square, Vancouver, B.C. V5Z 4B3, Canada

Frans Roes' article in the March 1994 issue is excellent but contains one mistake in asserting too assuredly "more males than females are conceived."

This was widely believed in the 1960s, since it is true that at 16 weeks of gestation the sex ratio is high-- 120:100 or higher. But this probably results from a preceding period of preferential female loss, so that the ratio at conception may be closer to 1:1 than was previously thought.

Mikamo (1969) studied the sex chromatin of 736 induced abortuses. For those 108 of less than 53 days ovulation age, he found a surplus of females, 64:100. Ounsted (1972) summarizes this and other findings supporting the notion of a female surplus around four weeks' gestation.

It seems likely that there are equal numbers of androsperms and gynosperms. Admittedly this does not ensure equal XY and XX conceptions, but the female surplus at four weeks could result from an initial preferential loss of XYs, which are believed to form higher up in the oviducts than XXs. This very early preferential loss of male concepti could result from ectopic nidations high up in the tubes. It is plausible that some may die and be resorbed without causing clinical symptoms.

From 4 to 16 weeks there would seem to be a preferential female loss because of less aggressive nidation, possibly from a greater antigenic difference between mother and son as compared with mother and daughter, as suggested by Ounsted. This phase ends at 16 weeks with the agreed surplus of males, who thereafter suffer a preferential loss--from

about 120:100 to 105:100 at birth, continuing into adulthood.

More may have been written on this subject in recent years.

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BOOK REVIEWS

The Tinbergen Legacy

By M. S. Dawkins, T. R. Halliday, and R. Dawkins, Eds. Chapman & Hall, London, 1991.

Reviewed by Laura Betzig, Evolution and Human Behavior Program and Museum of Zoology, University of Michigan, Ann Arbor, MI 48109 USA.

This is a nice little book. Tinbergen died on 21 December 1988 and, with characteristic modesty referred to throughout these chapters, he insisted that no service--secular or religious--be held. Instead, some 120 friends, colleagues and kin converged on Oxford on 20 March 1990 for a "memorial conference." Aubrey Manning, in a well-put "Afterword," mentions the Tinbergens' "extended ethological family," and Richard Dawkins, in a typically apt "Introduction," refers to the "Athens of ethology" that centered in the Tinbergens' home, Friday evenings especially, at Oxford from the 1950s on. Evidently, the conference had the feel of a family reunion; this book has a family feeling, too.

At the conference, eight people stood up to represent the Tinbergen legacy. Their papers are printed here. They include: Gerald Baerends on the Dutch origins of ethology; Nick Davies on (among other things) ethology

and behavioral ecology; Robert Hinde on ethology in *Homo* and other species; Felicity Huntingford on "Causation," or mechanisms; John Krebs on animal communication; Juan Delius on culture; Michael Robinson on comparative studies; and Larry Shaffer on "The Tinbergen Legacy in Photography and Film."

Tinbergen's legacy is both specific and general. The specific legacy, like many, has often been superseded. As Huntingford points out graphically, papers on animal behavior published in major journals over the last four decades--specifically, in *Animal Behaviour*, *Behaviour*, and *Ethology*--have focused less and less on motivation, external stimuli and other mechanistic issues, and more and more on function. As Krebs says, many views expressed in Tinbergen's standard 1952 paper on communication "are very different from present-day ideas," so much so that the connections are not at all easy to trace. And as Baerends notes, Lorenz's "innate vs. learned" dichotomy has given way to a greater respect for ontogeny, while his idea that mechanisms "did not overlap" has yielded to a hierarchical view of how behaviors are produced.

On the other hand, Tinbergen's general legacy has amplified and spread. These papers refer again and again to his insistence on the importance of getting to know an animal intimately in its natural environment, to his precision of thought and experimental work, and to the breadth of his approach--to the "four fields" described in his classic 1963 paper "On aims and methods of ethology." Through his own scholarly work, through his direct contact with students at Oxford and Leiden, and through his influence on popular pictures, film, and books, Tinbergen--as much as anyone before or since--made the study of animal behavior a respectable endeavor. That legacy will last forever.

For me, the nicest thing about this little book is its air of nostalgia. It often reinvoke the intoxication of being intellectually out front and in the center. I like to think I've lived in an Athens myself; I can't imagine any feeling could be better.

Frustration Theory: An Analysis of Dispositional Learning and Memory.

By Abram Amsel. Cambridge University Press, Pitt Bldg., Trumpington Street, Cambridge CB2 1RP, U. K.; 40 W. 20th St., New York, NY 10011 USA, 1992. £35.00 (hdbk.).

Reviewed by Eric A. Salzen, Dept. of Psychology, King's College, University of Aberdeen, Aberdeen AB9 2UB, Scotland.

A scientific lifetime of persistence with the problem of persistence. This is not an epitaph, but rather an expression of respect for Abram Amsel's review of some forty years of experimental study and theoretical development concerning the seemingly paradoxical behavioural effects of inconsistent reward, including the so-called "partial reinforcement extinction effect" (PREE). Since frustration theory and a major part of the experimental work in this field have originated from either Amsel, his students, or collaborators, the author has provided a personal example as well as a theoretical framework for the understanding of persistence as a behavioural trait or disposition. As he points out in the preface to this *magnum opus*, his approach may be considered "old-fashioned" since, like Hullian learning theories of the 1940's based on data from the laboratory rat, it is expressed in terms of the association of stimuli and reinforcements (S's and R's) rather than following the current penchant for the higher order concepts of "cognitive processes" which have arisen from learning studies with humans and other primates.

Psychologists of Amsel's generation may feel happier with S-R associations and conditioned learning as explanatory concepts because of their familiarity, but younger researchers might also consider their use as they can be more easily equated with the operation of real neuronal systems than the more abstract (one could even say mystical) components of a cognitive processing approach. The distinction between habit and memory first made by William James (and recently rediscovered and given a variety of new dual terminologies such as procedural versus declarative learning) may serve to reconcile this generational and conceptual divide. Amsel's S-R explanations of frustration effects in learning apply to what he

calls "dispositional" learning, which he recognises as yet another term for procedural learning. It may be that "cognitive process" explanations are therefore more appropriate in the case of declarative learning involving episodic memory mechanisms.

The behavioural effects of frustrative non-rewards include arousal, suppression, persistence, and regression to previously effective responses. The primary, or unlearned, effect is increased arousal, and according to Amsel's theory the internal stimuli from this frustration effect become associated with (i.e., conditioned to) approach responses that are being intermittently reinforced. Amsel calls this "countercondition", and the effect is that of secondary, or incentive, motivation. This may be relevant to human ethology because it provides a mechanism by which emotional arousal becomes a source of motivation. Amsel also believes it provides a developmental explanation for individual dispositions or character traits such as persistent responding or suppression of behaviour in the face of frustration.

After introducing the concepts of reward-schedule effects and dispositional learning, Amsel devotes two chapters to a review of S-R theories of motivation and associative learning, and a discussion of the nature and explanatory scope of frustration theory. He then reviews experimental data (mostly from single and double runway rat learning studies) showing the effects of partial reinforcement on the learning of persistence and its retention and transfer across situations and motivational states. Frustration theory is then used to analyse and explain the process of discrimination learning in which the differential cue stimulus for non-reward is an external one, rather than the internal stimulus of the frustration state which operates in single goal stimulus reward schedule studies. There then follows a consideration of alternative theories that can also account for PREE effects, but not for the more general phenomena of arousal, persistence, suppression, and regression, which are explained or predicted by frustration theory.

Having established a theory that explains a variety of reward schedule effects in adult rats, Amsel and his students and co-workers embarked on some developmental studies. In a series of technically elegant experiments with neonatal and weanling rats, they showed that there is a developmental sequence of emergence

of conditioned frustration responses. At first the unlearned response is one of persistent appetitive approach, which becomes transformed into conditioned persistence (dispositional learning) as the rat pup leaves the mother and encounters variation in reward presentation or magnitude. This development is paralleled by the development of habituation and responses to novelty, and is also accompanied by neuronal differentiation in the hippocampus. Conditioned inhibition (or the ability to suppress or delay responding) appears at a later age, and coincides with the development of cholinergic brain systems.

The development of the hippocampus and of hippocampal activity is reviewed in relation to behavioural inhibition theories of hippocampal function, dispositional learning, and behavioural development. The evidence suggests that the infant rat behaves much like a hippocampally damaged adult. A series of studies from his own laboratory of defective hippocampal development produced by foetal X-ray and alcohol exposure supports the notion that learned persistence develops as a result of infantile experience of reward probabilities and that it becomes a permanent disposition, or temperamental trait. The psychobiological evidence and arguments for the theory are then summarised in a separate chapter.

In the final chapter, Amsel makes explicit the possible applications of the findings on reward schedules to the care of human infants and to their personality development with respect to responses to frustration and punishment. He also suggests that the attention-deficit hyperactivity disorder results from slower counterconditioning of frustration responses (arousal and attention) to the goal response, so that the initial arousal remains free to attach to alternative stimuli giving response switching, i.e., hyperactivity and inattention. The paradoxical effects of stimulants on these children can also be explained if the stimulants differentially activate approach responses rather than avoidance responses. The strength and distinctiveness of Amsel's frustration theory is that it is applicable not just to the PREE and a variety of other reward-schedule effects, but also to dispositional (procedural) learning, many drug and lesion effects on behavioural development, and the development of the persistent personality.

This book is particularly useful as it both

summarises an extensive S-R associationist literature, and shows through simple S-R mechanisms how reward schedule, frustration, and punishment effects can account for the motivating and reinforcing effects of emotion produced by frustration. Amsel's work also points to neurophysiological mechanisms for the effects of early experience in establishing response dispositions associated with primary motivational systems. These are not to be confused with the effects of specific events and traumata in infancy and childhood. The latter involve episodic learning and memory systems and have their subsequent effects by mnemonic reactivation of their associated emotional states. This is probably not a book for the majority of human ethologists, but it will reward those with an interest in frustration behaviour and in the effects of early experience on personality development and its pathology.

The Nature of the Sexes: The Sociobiology of Sex Differences and the "Battle of the Sexes"

Edited by J. M. G. van der Dennen. Origin Press, Groningen, The Netherlands, 1992, 292 pp.

Reviewed by Vern L. Bullough, 17434 Mayall St., Northridge, CA 91325 USA

The 11 papers in this volume were originally part of the program for the 1988 Oslo meeting of the European Sociobiological Society. Three of the papers are by van der Dennen, the editor; two of these deal with aggressive behavior, while the third proposes an evolutionary rationale underlying the "battle of the sexes." Also dealing with aggression--and sex differences--is a paper by Tore Bjerke. All three papers on aggression emphasize the greater aggressiveness of the male.

Taking a somewhat different tack is Vincent Falger, who looks at sex differences in international politics as enacted in "Diplomacy," a board game in which teams of men, of women, and of both sexes compete with each other. The main result was that male teams were often winners or losers, while female teams often finished second. Doing best

of all were mixed-sex teams. While the sample is much too small to draw any overwhelming conclusion, Falger theorizes that the female choice approach is much more important to survival than is male competition for power.

The question that has to be asked, however, is whether biology or social conditioning is at work. Why did some female teams win? This emphasizes a critical failure of many researchers into sociobiology who make broad generalizations and often ignore the exceptions. Though these too can be explained by biological or experiential factors, it would seem that a necessary next step in sociobiology is to look at differences within the sexes instead of just comparing them with each other. Why did some female teams fare better than others, and why did not all mixed teams do as well as the average?

Other contributors include Peter Meyer, who looks at cultural universals in the making of sex identities; Robin Russell, Pamela Wells, Glenn Weisfeld and Carol Weisfeld, who examine differences between husbands and wives; and Bobbi Low, who reports on men and women, resources, and politics in pre-industrial societies. All three essays strive to separate biological factors from cultural ones, but not entirely successfully. Some of the studies apparently are based on the Human Relations Area files, and many of these are biased by the perceptions of the observers. Several citations in some of them have been outmoded by later studies.

What seem to be needed, as Peter Meyer emphasizes, are more biological studies that highlight some basic sex differences in behavioral dispositions, particularly in humans. But we also need more studies of the cultural and socialization process by researchers who are aware of biological factors.

The collection concludes with Ullica Segerstråle's essay on feminism and sociobiology. She argues that feminist criticism of sociobiology brought together various strands of feminism and also different factions of the Left. Such attacks, she holds, have led these critics into positions that appear intellectually difficult to defend. Perhaps for this reason, both the Left and

feminists have turned to attacking the epistemology of science itself. This she feels is a dead end for both the Left and feminists.

Intelligent criticism of sociobiology by these individuals, however, could be important to the progress of sociobiological research. Certainly the early animal researchers were very male centered, so much so that many of the studies were male biased. This has been corrected in later studies, but there is still a need for scientists to discuss more openly and candidly their uncertainties about their research and possible alternative interpretations.

The basic problem is that the potential data are just too immense for any one individual or discipline to encompass. This means that the whole field of sociobiology has to extend its horizons to include a number of other disciplines in order to access data available only to the specialist. More research is needed, to be sure. But so is more formal and informal discussion between sociobiologists and their critics, and fewer polemics. Certainly this book avoids polemics and tries to extend the areas of sociobiology ever further. But it remains an example of the committed talking to the committed.

ANNOUNCEMENTS

Evolutionary Theory

Evolutionary Theory publishes research and theoretical articles, comments, speculations, etc. of any length on ecology, paleontology, population genetics, plant and animal systematics, molecular evolution, comparative physiology and behavior, anatomy, biological philosophy and history, comparative cytology, anthropology, developmental patterns, and biogeography, among other fields. It is inexpensive and is published irregularly, as warranted by submissions received. A volume consists of 300 to 400 pages and costs \$26 (\$16 for those with incomes less than \$15,000/yr.). Subscription applications and papers should be sent to the journal at Dept. of Ecology & Evolution, University of Chicago, 1101 E 57th St., Chicago, IL 60637 USA. Editor is Leigh M. Van Valen of that department.

Politics and the Life Sciences

Many ISHE members are familiar with *Politics and the Life Sciences*, the international journal of the Association for Politics and the Life Sciences. Published semi-annually in February and August, *PLS* is a peer-reviewed, multidisciplinary journal with readers in more than twenty countries. Its mission is to advance knowledge of politics and promote better policy making through multidisciplinary analysis that includes the life sciences. Membership in APLS includes a subscription to the journal, a semi-annual newsletter about the association, conferences and other developments; a yearly membership directory; and other occasional mailings. Membership dues for 1994 are \$35 for individuals (\$20 for students). For additional information about the journal, membership, or submitting a manuscript, contact Gary R. Johnson, Editor, *Politics and the Life Sciences*, Lake Superior State University, Sault Ste. Marie, MI 49783-1699 USA; tel. 1-906-635-2757; fax 1-906-635-2111, e-mail pls@acs.saultc.on.ca.

Bradley Jesness

The work of ISHE member Bradley Jesness has been cited in *Who's Who in Engineering and Science*. His publications include "A human ethogram: its scientific acceptability and importance," and "Information processing theory and perspectives on development: view of a developmental ethologist." Both are indexed in *Resources in Education* (Nov. 1985 and May 1986 respectively) and are available on microfiche in libraries. To obtain a list of editorial corrections, contact him at 3513 Dupont Ave. S., #412, Minneapolis, MN 55408 USA, tel. 1-612-823-5934.

Developmental Colloquium

"Conception, naissance et petite enfance, aspects biosociaux" is the theme of a colloquium scheduled for 21-24 September 1994 in Marrakech, Morocco. Contact Prof. Emile-Crognier, C.N.R.S., U. R. 221, Pavillon de l'Enfant, 346 route des Alpes, 13100 Aix-en-Provence, France, tél. 33-42-23-57-94, fax 33-42-21-13-31.

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June 1994

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